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Aquatic Plant Control Research Program

Potential Use of Native Aquatic Plants for Long-Term Control of Problem Aquatic Plants in Guntersville Reservoir, Alabama

Report 2
Competitive Interactions Between Beneficial and Nuisance Species

by Robert D. Doyle, R. Michael Smart

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Prepared for Headquarters, U.S. Army Corps of Engineers

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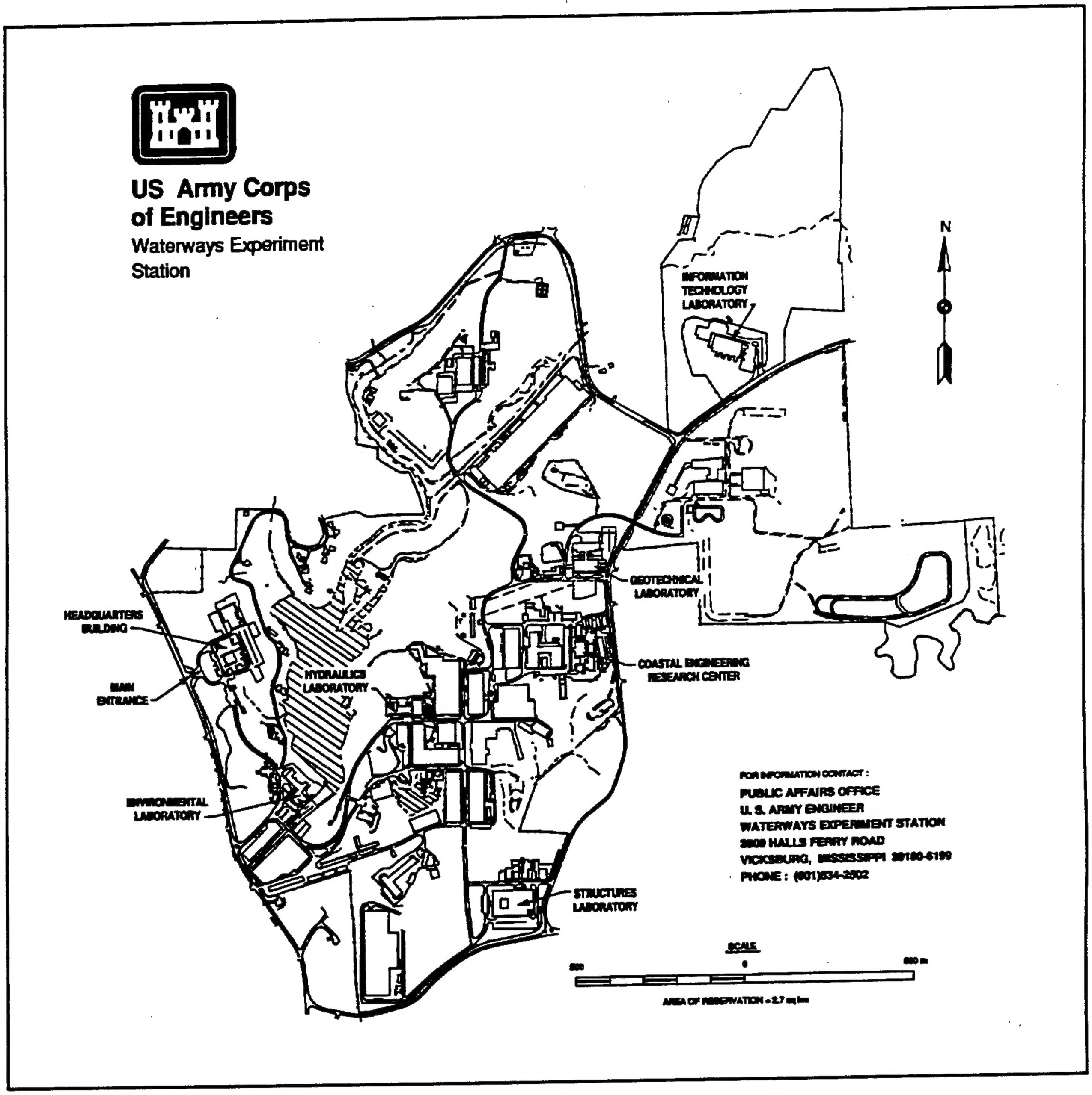

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Contents

Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP), Work Unit 32736 (Plant Competition). The APCRP is sponsored by the Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of the Army Appropriation No. 96X3122, Construction General. The APCRP is managed under the Environmental Resources Research and Assistance Programs (ERRAP), Mr. J. L. Decell, Manager. Mr. Robert C. Gunkel, Jr., was Assistant Manager, ERRAP, for the APCRP. Program Monitor during this study was Ms. Denise White, HQUSACE.

Principal Investigator for this study was Dr. R. Michael Smart, Ecosystem Processes and Effects Branch (EPEB), Environmental Processes and Effects Division (EPED), EL, WES. The report was prepared by Dr. Robert D. Doyle, who was assigned to the EPED under an Intergovernmental Personnel Act Agreement (IPA) with the Institute of Applied Science, University of North Texas, Denton, TX, with contributions from Dr. Smart. Experimental design, data analysis, and interpretation were provided by the authors. Dr. David Webb, Mr. Doug Murphy, and Mr. Leon Bates of the Aquatic Biology Department, Tennessee Valley Authority, contributed to experimental design and field data collection. Logistical support was provided by TVA, and TVA's Guntersville Reservoir Aquatic Research Facility (GRARF) at Langston, AL, was used to support field operations. Technical assistance was provided in the field by Mr. Larry Mangum, TVA; Messers. David Brewster, Mark Dowdy, Stuart Goldsby, and Jim Luken, Fish and Wildlife Associates, Inc.; Mr. Stephen McClintick, WES Lewisville Aquatic Ecosystem Research Facility (LAERF); and Mr. Tim Lee, Clemson University. Laboratory operations, data analysis, and report preparation were conducted at LAERF located in Lewisville, TX. Technical assistance in the laboratory was provided by Mr. David Honnell, AScI Corporation, and Mses. Aleida Eubanks, Susan Dutson, and Karen Kuhler, LAERF. Mr. McClintick and Ms. Lisa Stewart, LAERF, provided assistance with data analysis and graphics. The report was reviewed by Dr. Gary Dick and Mr. David Honnell, AScI Corporation.

This investigation was performed under the general supervision of Dr. Richard E. Price, Chief, EPEB, Mr. Donald L. Robey, Chief, EPED, and Dr. John W. Keeley, Director, EL.

At the time of publication of this report, Director of WES was Dr. Robert W. Whalin. Commander was COL Bruce K. Howard, EN.

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Conversion Factors, Non-SI to SI Units of Measurement

Non-SI units of measurement used in this report can be converted to SI units as follows:

Multiply	By	To Obtain
acres	4,046.873	square meters
inches	2.54	centimeters

1 Introduction

Although some species of aquatic plants present significant management problems, most species benefit the environment by stabilizing sediments, improving water clarity, removing excess nutrients and pollutants from the water, moderating shoreline erosion, and providing quality food and habitat for fish, waterfowl, and other organisms. However, aquatic plants that form dense, thick canopies or mats at the water surface can negatively impact the ecological and economic values of a water body. These growth forms prevent full utilization of the water body's potential by restricting exchange of gases between water and air, resulting in degraded water quality and poor habitat, and by interfering with navigational and recreational uses of the lake or reservoir. In Guntersville Reservoir, these growth forms are exhibited by both the weedy, nonnative aquatic macrophyte *Myriophyllum spicatum* (Eurasian watermilfoil) and the nuisance, albeit native, mat-forming cyanobacteria *Lyngbya wollei* (lyngbya) (Doyle and Smart 1993a).

Most widespread management problems are associated with nonnative species that are specialized for growth in disturbed environments. When the growth of these nuisance plants interferes with reservoir operations, available control options may further limit long-term management of the system by introducing additional disturbances (i.e., drawdowns, herbicides, and mechanical harvesting) in an effort to provide short-term, localized relief (Smart and Doyle, in preparation). To minimize the need for intensive control efforts, managers must develop long-term, ecologically based management plans to keep nuisance species from developing into large-scale problems.

One potential management option that preserves the benefits of having plants in a reservoir, but avoids most serious management problems associated with excessive growth, is the establishment of native aquatic plants to minimize the growth of nuisance species. Although aggressive exotic species, by virtue of their widespread success, have often been considered highly competitive species, research has demonstrated that some native plants are actually much more competitive. Short-term greenhouse and pond-scale research has demonstrated that some species of native plants, when well-established, are able to resist invasion by nuisance species such as *Hydrilla verticillata* (hydrilla) and *M. spicatum* (Smart 1992; Smart 1993; Smart, Barko, and McFarland 1994). The competitive superiority of *Potamogeton americanus* over *H. verticillata* under low nitrogen conditions has also been demonstrated

(McCreary, McFarland, and Barko 1991). Research conducted within this work unit provided field evaluations of the ability of several native plants to resist invasion by nuisance exotic species under reservoir conditions.

The field portion of this research was conducted in Guntersville Reservoir, Alabama, as part of the Joint Agency Guntersville Project (JAGP) that authorized a 5-year cooperative aquatic plant management project on Guntersville Reservoir between the Tennessee Valley Authority (TVA) and the U.S. Army Corps of Engineers (Bates, Decell, and Swor 1991). Guntersville Reservoir is the second largest of the Tennessee River reservoirs and is operated by TVA. Located primarily in northeastern Alabama, the reservoir impounds 67,900 surface acres[1] and is authorized for power production, commercial navigation, and flood control, with secondary uses to include fish and wildlife habitat, water supply, and recreation. The history of aquatic management problems associated with the growth of exotic species, in conjunction with conflicting management demands of this multipurpose reservoir, made it a useful site to serve as a National Demonstration Project for innovative aquatic plant management strategies (TVA 1992).

Research conducted under this work unit had two major objectives:

a. To evaluate methods for promoting the establishment and persistence of populations of native aquatic plant species in Guntersville Reservoir.

b. To evaluate the ability of established native plant populations to resist reinvasion by nuisance species.

Results of research addressed the methods found necessary to establish beneficial native populations in Guntersville Reservoir and are described in Report 1 of this series (Doyle and Smart 1993a). The establishment phase of the research took place during 1991-1992, a period when grass carp were stocked into Guntersville Reservoir and a time of general decline of the aquatic macrophytes in reservoirs throughout the Tennessee River system (Webb et al. 1994). During this period, the macrophyte community in Guntersville reservoir reached its lowest abundance of the decade (Webb et al. 1994), and the sites utilized for research were completely devoid of submersed aquatic plants. This made establishment efforts difficult because of increased turbidity caused by wind resuspension of the bare sediments and the concentrated attention of various herbivores on the experimental plots, which contained the only submersed aquatic vegetation in the embayments.

This report is the second and final report of the series and will focus on objective *a*. Specifically, this report will detail results of three research efforts to document competitive interactions between established populations of beneficial native plants and nuisance species. This phase of research focused on

[1] A table of factors for converting non-SI units of measurement to SI units is presented on page vii.

the competitive interactions of *M. spicatum* with *Vallisneria americana* (wild celery) or *Potamogeton nodosus* (American pondweed) (Chapter 2), *M. spicatum* with *Nelumbo lutea* (American lotus) (Chapter 3), and *L. wollei* with *Pontederia cordata* (pickerelweed) or *P. nodosus* (Chapter 4). Each research effort took place at different sites in Guntersville Reservoir (Figure 1) and is treated independently in the chapters to follow.

2 Competitive Interactions Between *Vallisneria americana* or *Potamogeton nodosus* and *Myriophyllum spicatum*

Introduction

Myriophyllum spicatum is a submersed macrophyte that was introduced to North America from its native range in Europe, Asia, and North Africa, and quickly became a widespread problem (Couch and Nelson 1985). Once established, this evergreen perennial spreads rapidly to adjacent unvegetated areas by the formation of autofragments (Grace and Wetzel 1978; Madsen, Eichler, and Boylen 1988; Smith and Barko 1990) or radial expansion of colonies (Madsen et al. 1991). The canopy-forming morphology and aggressive growth of this species can result in significant negative impacts to lakes ecosystems (Newroth 1985; Madsen, Hartleb, and Boylen 1991).

The prolific growth of exotic species has caused Guntersville Reservoir to experience the most severe aquatic plant management problem of the TVA system (TVA 1992). TVA records indicate that submersed aquatic plants were sparse during the years following construction in 1939. However, in the early 1960s, *M. spicatum* began to proliferate in the system and continues as a major impediment to the multipurpose reservoir use. In 1988, this species covered approximately 6,000 ha of the lake (Webb et al. 1994).

This study was conducted in Chisenhall Embayment (Figure 1), a small cove on Guntersville Reservoir historically dominated by *M. spicatum*. Since the establishment took place during a period when *M. spicatum* was not present in the embayment, this research provided a field trial of the abilities of newly established plots of native submersed or floating-leaved plants to resist reinvasion by *M. spicatum*.

Methods

The establishment phase, described in detail elsewhere (Doyle and Smart 1993a), took place during 1991-1992, a period of general decline of *M. spicatum* throughout the Tennessee River system and Guntersville Reservoir in particular (Webb et al. 1994). Native species were planted in small (1.5- by 1.5-m) plots within a larger exclosure (20- by 30-m). Because the embayment was devoid of other vegetation during the establishment period (Photo 1), and because the native species utilized rank high on the food-preference orders of common herbivores such as slider turtles and muskrat, exceptional difficulty was experienced in establishing the plots. However, after replanting and initiating a muskrat and turtle trapping effort, by late summer of 1992, some success was achieved in establishing the native plants.

In the spring of 1993, four species were replanted in the plots at Chisenhall where visual observations indicated poor establishment in 1992 (Table 1). Two distinct ecotypes of *V. americana* were utilized for this effort. The more common perennating perennial ecotype, which produces winter buds in the fall and is dormant during the winter, was planted in five plots. The evergreen perennial ecotype (see Smart and Dorman 1993), which does not produce winter buds and remains green throughout the year, was planted in three plots. A fourth plot of the evergreen perennial ecotype of *V. americana*, previously planted in 1992 and which was particularly well established, was not replanted. Although the complete range of this ecotype of *V. americana* is unknown, it appears to be common in Florida and Texas and may be widely distributed along the Gulf coast states. Five plots of each of the other species were planted. With the herbivore trapping program instituted, all species began to grow well except *Potamogeton pectinatus* (Sago pondweed), which failed to sprout from the planted tubers.

During 1993, *M. spicatum* began to regrow within the exclosure at Chisenhall and, by late summer, had begun to top out. Although a few *M. spicatum* plants were observed outside the exclosure, the embayment remained virtually devoid of plants. In August 1993, a single 0.25-m^2 quadrat was harvested from each of the planted plots, and six quadrats were harvested from unplanted areas between plots to serve as controls for the regrowth of *M. spicatum* in the absence of competition from natives. Aboveground biomass was sorted by species and dried to constant weight at 60 °C.

During 1994, *M. spicatum* began to regrow throughout Guntersville Reservoir and once again completely dominated Chisenhall Embayment. No additional plantings were made in 1994 and the exclosure fencing was removed, so that the planted plots were unprotected from herbivory by turtles, muskrat, or grass carp. In August 1994, a visual survey of the plots was made. Although there were scattered pockets of *P. nodosus*, *Heteranthera dubia* (water star grass), and *V. americana* within the exclosure, only one of the *V. americana* plots appeared to be vigorously established and expanding despite herbivory and the regrowth of *M. spicatum*. This plot was the same plot of the

evergreen perennial *V. americana* that had been growing well at the beginning of the year. *Vallisneria americana* plants within this plot were growing beyond the original boundaries of the plot, and far fewer *M. spicatum* plants occurred within the plot than in the surrounding area. To document the apparent success of this well-established *V. americana* at minimizing the regrowth of *M. spicatum*, three 0.25-m^2 quadrats were harvested from within this plot along with three others adjacent to it to serve as controls.

Results and Discussion

The results of the August 1993 biomass harvest indicated varying degrees of success in establishment of native species (Figure 2). The least satisfactory results were obtained from *P. pectinatus*, which was never observed to have sprouted from the dormant tubers planted. *Heteranthera dubia* and the perennating perennial ecotype of *V. americana* began to grow after planting, but most of the plots never became very well established. Not surprisingly, the growth of *M. spicatum* was not competitively inhibited in the plots planted with these species, and the mass of *M. spicatum* within these plots was not significantly lower than in the controls.

Greater success was achieved in establishing *P. nodosus* (Figure 2). However, despite fairly high *P. nodosus* biomass within the plots, the mass of *M. spicatum* was not significantly lower than in control plots. Although this may indicate that *P. nodosus* is not an effective competitor with *M. spicatum*, these results were probably due to the small plot size utilized in this study. *Potamogeton nodosus* is likely to successfully compete with submersed species primarily through establishing a leaf canopy at the water surface to shade out the plants growing beneath it. With the small plot sizes utilized, this potential competitive advantage of *P. nodosus* was not realized, and *M. spicatum* grew well. Future research on the competitive interactions of these two species should be performed in such a way that the light-shading advantage of *P. nodosus* is achieved.

The evergreen perennial ecotype of *V. americana* showed some encouraging results, with three of four plots exhibiting successful establishment during 1993. When all four plots of the ecotype are considered, the mass of *M. spicatum* was lower than in the control plots, although the statistical strength of this relationship was not strong ($p = 0.13$, Figure 2). However, the very small sample size and variable nature of the data belie the significance of the interaction between the two species. Additional evidence that *V. americana* is a potentially good competitor against *M. spicatum* under field conditions is provided by analyzing the same data in a different way. If the *V. americana* plots (regardless of ecotype) that were judged to be moderately well established ($n = 4$) are separated from those that obviously were not ($n = 5$), an interesting pattern emerges (Figure 3). In this case, comparison of *M. spicatum* biomass in the established *V. americana* plots with *M. spicatum* biomass in controls indicates a significant reduction of *M. spicatum* growth ($p = 0.04$).

Predictably, in plots where *V. americana* was not well established, the mass of *M. spicatum* was not lower than in the control plots ($p = 0.88$).

In August of 1994, the biomass of *M. spicatum* in the single surviving plot of *V. americana* remained significantly lower than in adjacent unplanted areas (Figure 4). However, the loss of three moderately established plots of *V. americana* between 1993 and 1994 is cause for concern. Because the exclosure fencing had been removed in early 1994, these failures were thought to be due to selective herbivory rather than the influence of *M. spicatum* regrowth. Clearly, in areas where herbivory is expected, small plots of natives like the ones utilized for this study do not provide the long-term resiliency needed.

Despite the complicating factor of herbivory, these results support conclusions reached on the competitive ability of *V. americana* in greenhouse and pond-scale research. In greenhouse studies, when *V. americana* is well established in containers and allowed to preempt available resources, it is able to prevent the development of nuisance levels of *H. verticillata* (Smart 1993; Smart 1992; Smart, Barko, and McFarland 1994). When *V. americana* is allowed a preemption period, the outcome of 9 weeks of competitive growth favors *V. americana* by a large margin (93 percent *V. americana*: 7 percent *H. verticillata*). However, when both plants are planted at the same time, which allows no preemptive establishment of *V. americana, H. verticillata* completely dominates the competitive interaction (5 percent *V. americana*: 95 percent *H. verticillata*). Intermediate levels of preemptive establishment by *V. americana* result in intermediate dominance. Likewise, in pond research, *V. americana* populations were able to effectively resist invasion by *H. verticillata* and *M. spicatum* only when allowed several months of preemptive establishment.[1]

The results of the research reported here are encouraging in that they appear to confirm the principle of competitive advantages based on preemptive establishment of *V. americana*. This principle, first demonstrated in greenhouse and later pond-scale studies, also appears to hold true in these field trials. As more is learned about how to efficiently establish native plants in the field and how to selectively control nuisance plants with herbicides or biological controls, the ultimate goal of providing reservoirs with healthy, resilient communities of beneficial native plants will be closer.

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[1] Personal Communication, 1994, R. M. Smart, Ecologist, U.S. Army Engineer Waterways Experiment Station, Lewisville Aquatic Ecosystem Research Facility, Lewisville, TX.

3 Competitive Interactions Between *Nelumbo lutea* and *Myriophyllum spicatum*

Introduction

Nelumbo lutea (American lotus) is a native emergent/floating leaved species that has the potential for competing effectively with nuisance submersed aquatic plants, primarily by virtue of its ability to shade submersed plants. Although itself an aggressively growing plant and not desirable in high-use areas, *N. lutea* may be useful for producing "gaps" within large monospecific beds of submersed exotic plants such as *M. spicatum*. These gaps would provide some structural diversity in an otherwise monotypic habitat. *Nelumbo lutea* is easily controlled by a wide variety of approved aquatic herbicides (Westerdahl and Getsinger 1988) should this become necessary or desirable.

Methods

Small plots of *N. lutea* were established at the Ossa-Win-Tha site by planting scarified seeds in small plots within a larger exclosure in 1991 and 1992 (Doyle and Smart 1993a). At the time of *N. lutea* establishment, there was no *M. spicatum* present within the cove, although it had a history of nuisance infestation (Table 2). By the summer of 1992, *N. lutea* had expanded to fill the exclosure; by 1993, the colony was expanding rapidly beyond the protected area (Photo 2). During 1993, there was an initial regrowth of *M. spicatum* within the cove; by August of 1993, the population was extensive enough to interfere with the small boat dock located in the cove (a priority treatment area). By request, TVA treated parts of the cove with an application of 2,4-D. Although the *N. lutea* colony suffered minor damage near the edges because of the herbicide treatment, most of the colony was unaffected. In the spring of 1994, the fencing that defined the original exclosure was taken down, although the *N. lutea* colony continued expansion, in ever-increasing concentric circles

around the original exclosure. At the same time, *M. spicatum* regrew throughout the cove. The fortuitous occurrence of *M. spicatum* regrowth into an area where *N. lutea* had been established provided an opportunity to examine the ability of the expanding *N. lutea* colony to withstand invasion by *M. spicatum*.

The development of the *N. lutea* colony was monitored by biweekly estimates of percent cover within two 1.2- by 2.4-m plots established in the original exclosure. Light penetrating through the *N. lutea* canopy to a depth of 10 cm was also determined from paired measurements of light above and beneath the plant canopy. Total incident light above the canopy was measured with a flat quantum sensor (photosynthetically active radiation-PAR, 400 to 700 nm), while underwater light was measured with a spherical PAR quantum sensor (LiCor). Seven light measurements were made from various positions within each plot in order to obtain an estimate of the average light climate. As the colony size expanded, the approximate distribution of the *N. lutea* colony was noted.

In August 1993, and again in August 1994, biomass harvests were conducted to quantify *M. spicatum* regrowth in relation to the developing *N. lutea* colony (Figure 5). In 1993, 14 quadrats (0.25 m^2) were harvested along two transects extending from within the original exclosure, through the developing colony, to 15 m beyond the edge of the colony. At the time of sampling, water depth along the transects varied between 50 and 70 cm. Aboveground biomass of each plant species within the quadrat was harvested, sorted by species, and dried to constant weight. In August 1994, a second harvest was conducted and ten replicate 0.25-m^2 quadrats were harvested in each of four zones within and near the colony. These zones corresponded to varying degrees of *N. lutea* establishment (Figure 5). The interior zone included the original plantings, and this portion of the colony was in its third or fourth year of growth. Plants in the second zone, the area to which *N. lutea* had expanded in 1993, were in their second year of growth. The third zone was the area to which the colony had expanded in the summer of 1994, and these *N. lutea* plants were in their first year of growth. The last zone was outside the colony. Plant materials collected were returned to the laboratory, sorted by species, and dried to constant weight at 60 °C.

Results and Discussion

The developing colony of *N. lutea* grew rapidly during the 3-year study period, expanding radially from year to year by rapid growth of stolons (Figure 5). During 1991-1992, planted plots of *N. lutea* became established and expanded to include most of the area within the original exclosure. In 1993 and 1994, the colony expanded rapidly beyond the exclosure. As the colony expanded, the newly colonized zones exhibited a sparse canopy of mostly floating leaves growing from the radial stolons. In subsequent years, the plant density in these areas increased and developed a dense *N. lutea* canopy composed of both floating and emergent leaves. Measurements of percent

surface cover and light penetration within the original exclosure area (Figure 6) demonstrate the increasing density of the colony within the original exclosure between 1992-1993. The shading effect of its floating and emergent canopies is apparent; during most of the growing season, light penetrating the *N. lutea* canopies ranged between 1 and 10 percent of incident light.

Results of biomass transects, taken in 1993 in the Ossa-Win-Tha cove experienced a regrowth of *M. spicatum*, showed a strong inverse relationship between *M. spicatum* and *N. lutea* (Figure 7). Biomass of *M. spicatum* was very low within the interior of the *N. lutea* colony but increased exponentially towards its edges to a maximum biomass (outside the colony) in excess of 250 g dry mass m^{-2}.

The 1994 harvest also showed differences in *M. spicatum* biomass with respect to the degree of *N. lutea* establishment (Figure 8). In areas where *N. lutea* was well established (colony age 2 years or greater), the biomass of *M. spicatum* was very low. In sharp contrast, *M. spicatum* biomass was high outside the colony and in the area where *N. lutea* was just beginning to grow. These last two zones represent the regrowth of *M. spicatum* with little or no competitive interference from *N. lutea.* These data show that *N. lutea* effectively outcompeted the submersed species and was able to competitively exclude the nuisance plant by preempting resources within areas where the colony was established.

Although mechanisms by which *N. lutea* competitively excluded *M. spicatum* were not rigorously investigated, light appeared to be an obvious factor. *Myriophyllum spicatum* is a species that requires a high light environment and is intolerant of shade (Madsen et al. 1991). Once well established, floating and emergent canopies of *N. lutea* reduced light penetration to less than 10 percent of the incident solar radiation (Figure 6). This resulted in PAR levels beneath the *N. lutea* canopy of 200 $\mu Em^{-2}s^{-1}$ or less during the day, a value below that needed for *M. spicatum* to maintain a positive (whole plant) daily carbon balance. Madsen et al. (1991) have modeled the daily carbon balance of this species in Lake George, New York, and conclude that, because of the high light requirements of *M. spicatum*, the daily balance would become negative at a depth where the maximum daily irradiance was less than 600 $\mu Em^{-2}s^{-1}$. Warmer temperatures common in Guntersville Reservoir would likely increase the daily respiration rate relative to the photosynthetic output of the species and increase minimum daily light requirements for this species. The light climate beneath the *N. lutea* canopy was much lower than that required by *M. spicatum*, but may be suitable for some shade-tolerant native species (Madsen et al. 1991).

4 Competitive Interactions of *Pontederia cordata* and *Potamogeton nodosus* with *Lyngbya wollei*

Introduction

Lyngbya wollei is a filamentous, mat-forming "giant" cyanobacteria that has received some attention in recent years because of the nuisance characteristics of its floating mats (Bowes, Spencer, and Beer 1990; Dick 1989; Speziale, Turner, and Dyck 1988, 1991). In Guntersville Reservoir and other southeastern lakes and reservoirs, *L. wollei* is a perceived nuisance that limits the recreational uses of portions of the reservoir and significantly detracts from the aesthetic appeals of littoral zones where it occurs (Doyle and Smart 1993a). Unlike most other cyanobacteria and filamentous algae, *L. wollei* often accumulates enormous standing crops. In quiet coves and backwaters, *L. wollei* may accumulate as high as 6 to 7 kg fresh weight/m^2 (Beer, Spencer, and Bowes 1986; Speziale, Turner, and Dyck 1988, 1991), values higher than most submersed and many emergent macrophytes.

Lyngbya wollei is unique among cyanobacteria primarily in its size and extreme resilience of its thick sheaths. Unlike typical bacteria, which are <1 µm in size, and other *Lyngbya* species, which are typically 2 to 5 µm in diameter, *L. wollei* cells are 24 to 65 µm in diameter (about the thickness of human hair); individual filaments may be up to a meter in length (Speziale 1994; Speziale and Dyck 1992). The thick sheaths are composed primarily of $CaCO_3$, which likely accounts for the propensity of this species for waters containing high levels of calcium.

Lyngbya wollei accumulates to nuisance levels because of its ability to grow and survive periods of poor growth conditions. Laboratory experiments on small samples have confirmed that this species shows numerous "opportunistic traits" including low-light requirements for photosynthesis, high temperature optima, insensitivity of photosynthesis to high O_2, and the ability to utilize bicarbonate (Beer, Spencer, and Bowes 1986; Beer et al. 1990; Speziale,

Turner, and Dyck 1991). Like other bacteria and cyanobacteria, this species seems able to survive long periods of poor environmental conditions. In fact, samples of *L. wollei* have been observed to survive even a full year in complete darkness.[1] While these characteristics have been described for isolated, small samples of *L. wollei* under laboratory conditions, the dynamics of the thick heavy mats in the field is poorly understood.

Lyngbya wollei is characterized by a blue-black color because of the abundance of red and purple phycobilin pigments, which, along chlorophyll *a* and carotenoid pigments, allows the organism to photosynthesize under low-light conditions. Unlike other cyanobacteria, *L. wollei* has a perennial life history with virtually all of the summer biomass accumulation overwintering as a benthic mat (Speziale, Turner, and Dyck 1991).

Lyngbya wollei present at the Waterfront site exhibits distinct seasonality in its vertical distribution. During the winter, when the level of the reservoir is down 30 to 50 cm, *L. wollei* exists primarily in two strata with a thick, cohesive benthic mat overlying numerous filaments buried within a highly organic layer of sediment. During the summer, about half of the mat floats to the surface, buoyed by trapped gas bubbles, and the cyanobacterial community is stratified into three distinct layers: floating mat, benthic mat, and filaments buried in the organic sediments.

The most obvious portion of the community (and the portion that causes water resource problems) floats at the surface and has a mass of up to several kilograms of fresh weight per square meter. The top layer of this floating mat consists mostly of dead cells that serve to shade the cells beneath from high light at the surface. The underside of this floating mat is composed of healthy, heavily pigmented cells with high photosynthetic potential (Speziale, Turner, and Dyck 1991). Like the undersurface of the floating mat, the benthic mat has a high biomass and is composed of live, healthy cells. These cells are heavily pigmented with phycobilins and are characteristically black. Finally, buried in organic sediments beneath the benthic mat are filaments of *L. wollei* that appear to survive long periods of time heterotrophically. This organic sediment layer is underlain by sandy sediments that contain only trace quantities of *L. wollei* filaments.

Experimental Objectives

This portion of the research contained two phases of work. The first phase took place between 1991 and 1992 and sought to identify native emergent or floating-leaved macrophytes that could survive within the littoral areas of Guntersville Reservoir dominated by *L. wollei*. The second phase took place

[1] Personal Communication, 1994, B. J. Speziale, visiting Assistant Professor, Clemson University, Clemson, SC.

between 1992 and 1994 and focused on monitoring the growth and expansion of successfully established macrophytes, the mass and spatial distribution of *L. wollei*, and the environmental conditions (light and sediment nutrients) within both vegetated and unvegetated plots at the Waterfront site (site with heavy *L. wollei* infestation, Figure 1). The objective of this second research phase was to evaluate the potential of native macrophytes to ameliorate the nuisance characteristics of the cyanobacterial mat.

Results of the first phase of research were summarized in the first report of this series (Doyle and Smart 1993a). Briefly, small plots of native floating-leaved or emergent macrophytes were planted within large exclosures at three sites on Guntersville Reservoir corresponding to sites with no, moderate, or heavy *L. wollei* mat developments. Although seven native macrophyte species were tested, only the emergent *P. cordata* and floating-leaved *P. nodosus* were suitable for establishment in areas with heavy *L. wollei* infestations. *Nelumbo lutea* and *Justicia americana* (American water willow) were both established at the site with moderate mats, while *Saururus cernuus* (Lizard's tail), *Eleocharis quadrangulata* (spike rush), and *Scirpus validus* (soft-stem bulrush) were successfully established only at the control site with no *L. wollei* mats (Doyle and Smart 1993b; Smart et al. 1993).

This second and final report in the series summarizes the effects of the two macrophyte species successfully established at the Waterfront site (site with heavy *L. wollei* mats) on the environmental conditions and the biomass distribution of *L. wollei* mass within the water column.

Methods

Establishment of native plants

The techniques used to establish *P. nodosus* and *P. cordata* are described in detail in the first report of this series (Doyle and Smart 1993a) and will only be briefly summarized here. Both macrophyte species were planted within small (1.2- by 2.4-m) plots within a larger (10- by 20-m) exclosure at the Waterfront site. Boundaries of 14 plots were initially defined by anchoring frames constructed of 0.5-in. polyvinyl chloride (PVC) pipe to the sediments beneath the benthic mat of *L. wollei*. Some of the plots were not vegetated during the current study period of 1992-1993, and unvegetated plots served as controls for the vegetated ones. These control plots served as references by which to measure the impact of the macrophytes on the distribution and mass of *L. wollei* (Figure 9).

Dormant tubers of *P. nodosus* collected during the winter from Cedar Creek Reservoir, Alabama, were planted in June 1991 in Plots 11 and 13, which had an average depth of about 75 cm. Thirty-two dormant rhizomes of *P. cordata* collected from Reelfoot Lake, Tennessee, were planted in Plots 7 and 8 in

March 1992. Average water depth in the plots was about 50 cm during the growing season.

The apparent success of the planted plots was evaluated by routine visual estimates of percent surface cover of macrophytes and *L. wollei* in vegetated and adjacent control plots. These estimates were made at 2-week intervals throughout the growing seasons of 1992 and 1993. In 1992, the percent cover was estimated within each of the two original plots of both macrophyte species. In 1993, *P. cordata* had expanded into two additional plots and was evaluated for each of the four plots. In addition, percent surface cover of *L. wollei* mats in adjacent unvegetated control plots was also recorded.

Biomass harvests

In addition to monitoring percent cover of plants, biomass samples were harvested in August of both 1992 and 1993 to quantify the effects of the macrophytes on the biomass distribution of *L. wollei*. In 1992, duplicate 0.06-m^2 samples (circular quadrat 28-cm diam) of *L. wollei* were collected from within each *P. cordata* plot, and triplicate samples were collected from each *P. nodosus* plot. *Lyngbya wollei* was collected separately from the floating mat and the benthic mat. Unfortunately, samples were not collected from the organic sediment layer to quantify the *L. wollei* mass within the sediments. In 1993, thirty-two 0.06-m^2 samples of *L. wollei* were collected from within the larger exclosure. Ten samples were located within the 20 percent of the exclosure where *P. cordata* was growing, six samples in the area where *P. nodosus* had grown the previous year, six from the deep control plots, and the remaining ten from the shallow control plots (Figure 9). As before, *L. wollei* samples were collected from the floating and benthic mats. In addition, sediment cores (4.4-cm diam) from beneath the benthic mat were collected to quantify the *L. wollei* biomass in the organic sediment layer. Biomass samples from the harvests were immediately returned to the laboratory, picked clean of debris, and dried to constant weight at 60 °C before weighing.

Environmental conditions within *P. cordata* plots

To understand possible competitive influences of established plots of *P. cordata* on the *L. wollei* mats, the effect of the macrophytes on the availability of both light and sediment nutrients to the mats was monitored. The effect of the macrophyte leaf canopy on light availability to *L. wollei* mats was quantified by measuring the light attenuation within vegetated plots. Light readings were taken simultaneously from a flat quantum PAR sensor in air and a spherical underwater quantum sensor positioned 0.1 m beneath the water surface. Seven separate measurements were made within each plot as the underwater sensor was carefully moved around so that a better estimate of the average light climate within the plot could be obtained.

To quantify the effects of the *P. cordata* on soluble nitrogen and phosphorus potentially supplied to *L. wollei* mats from the sediments, nutrient profiles were measured within vegetated (*P. cordata*) and adjacent unvegetated (*L. wollei*-only) areas several times during the growing seasons of 1992 and 1993. Each measurement was made by deploying an interstitial water sampler (peeper) constructed of 1-in.-thick acrylic and containing 12 individual collection cells (18 ml) on 2.5-cm interval centers. This effort resulted in nutrient profiles ranging from the overlying water, through the *L. wollei* benthic mat, through the organic sediment layer, and into the underlying sand. Before deployment, each cell was filled with deionized, deoxygenated water and covered with a nucleopore membrane (pore = 0.47 μm). At each sample date, multiple (2 to 4) peepers were deployed within vegetated plots and adjacent areas with only *L. wollei.* After deployment of 10 to 14 days to allow dissolved nutrient concentrations to equilibrate, the peepers were retrieved for analysis. Water samples were collected from each cell into 20-ml syringes and transferred to plastic bottles. Syringes and bottles were acid-washed and triple rinsed with deionized water prior to use. Each sample was preserved with 0.5 ml of 50-percent HCL and shipped on ice to the Lewisville Aquatic Ecosystem Research Facility (LAERF), Lewisville, TX, for analysis. Ammonium nitrogen (NH_4-N) was measured with an ion-selective electrode, while soluble reactive phosphorus (SRP) was measured using standard colorimetric procedures (American Public Health Association (APHA) 1992).

Container experiments

Because of a significant negative relationship between the presence of *P. cordata* and the mass of *L. wollei* observed during 1992 (see below), a controlled experiment was designed to test the short-term effect of macrophyte seedling growth on *L. wollei.* This experiment was conducted at the LAERF during the summer of 1993. Sediment, *L. wollei*, and *P. cordata* seeds were collected at the Waterfront site in Guntersville Reservoir and shipped to the LAERF. The *P. cordata* seeds were germinated in the laboratory and planted in the greenhouse in small (50-cc) peat pots in January 1993. In June 1993, an outdoor container experiment was set up to investigate the influence of *P. cordata* seedling growth on *L. wollei* mass.

Sediments collected from Guntersville Reservoir were homogenized and poured into 36 four-liter plastic containers. Containers were randomly assigned to one of six 400-ℓ plastic tanks so that each tank contained six 4-ℓ containers. The tanks were filled with Lewisville Lake water previously treated with alum to precipitate phosphorus to prevent the growth of filamentous green algae. Two tanks were randomly assigned to one of three experimental treatments: *L. wollei*, *P. cordata*, and *L. wollei* + *P. cordata.* Twenty-four *P. cordata* seedlings were selected for similarity in size (approximately 30 cm tall), and one seedling was planted in each container within the *P. cordata* and *L. wollei* + *P. cordata* tanks. After the seedlings had been planted, each 4-ℓ container was fitted with a 20-cm-tall cylinder of 0.5-cm mesh hardware cloth encircling each seedling (if present) and extending about

2 cm above the water surface. *Lyngbya wollei* subsamples were then packed into the mesh cylinders in the *L. wollei* and *L. wollei* + *P. cordata* tanks. The *L. wollei* mass added to each pot equaled 30 ± 2 g dry weight per pot, equivalent to 1,000 g dry weight m^{-2}, an approximate upper limit of *L. wollei* biomass sampled in Guntersville Reservoir.

Water levels in tanks were maintained by periodic addition of alum-treated lake water to offset losses because of evaporation and transpiration. The experiment continued for approximately 10 weeks between June 10, 1993, and August 16, 1993. At the conclusion, *P. cordata* and *L. wollei* (if present) biomass was collected separately and dried to constant weight at 60 °C. Samples were weighed and then analyzed for tissue nitrogen.

Results

Macrophyte growth

During 1992, *P. nodosus* and *P. cordata* grew well in the planted plots. By early summer, both species had grown and were forming healthy leaf canopies with 100-percent surface cover in the planted plots (Photo 3, Figure 10). *Potamogeton nodosus*, which was then in its second year of growth, quickly expanded to cover about 20 percent of the entire exclosure (Figure 9). Unfortunately, *P. nodosus* was seriously damaged in the early fall 1992 by muskrat herbivory. Visual observations confirmed that all of the *P. nodosus* plants had been either uprooted or cut off near the sediment surface. The timing of the incident likely preceded the onset of tuber formation, and the plant population was unable to recover in 1993, with only a few, scattered plants being observed during the year. Surface cover of *P. nodosus* in 1993 averaged only about 5 percent and never exceeded 20 percent of the 1.2- by 2.4-m plots within which it had been established (Figure 10).

Pontederia cordata also grew quickly in 1992, forming a dense, lush stand within the plots and producing flowers and seeds in profusion. Many seeds subsequently germinated and established during the spring of 1993. This recruitment of seedlings, coupled with transplanting of 50 additional plants in May of 1993, resulted in expansion of the *P. cordata* during 1993. In addition, many seedlings grew between the plots, eventually resulting in a contiguous stand of *P. cordata* covering about 20 percent of the entire exclosure (Figure 9).

L. wollei floating surface mat

Formation of a floating surface mat of *L. wollei* was significantly affected by the presence of the macrophytes. In contrast to adjacent deep control plots, which formed a thick surface floating mat in early July, the *P. nodosus* plots had less than 10-percent *L. wollei* surface coverage until mid-September when

coverage of *L. wollei* suddenly increased to 60 to 80 percent (Figure 11). This increase in *L. wollei* surface cover followed the muskrat disturbance to the *P. nodosus* population, when the percent cover of this native macrophyte dropped from 100 to 0 percent (Figure 10). *Potamogeton nodosus* regrew poorly in 1993, and, in the absence of macrophyte, the coverage of *L. wollei* in these plots was not different from that of the deep control plots throughout 1993 (Figure 11).

Pontederia cordata was also effective at preventing the development of a floating surface mat of *L. wollei* (Figure 12). In 1992, the macrophyte emerged in early May and, because of the relatively close spacing of the plants, formed a very dense leaf canopy above the water surface. By June, part of the *L. wollei* benthic mat in the shallow control plots had floated to the surface. Within *P. cordata* plots, however, none of the benthic mat floated to the surface, and the plant density kept the floating mats surrounding the plots away. This resulted in virtually no floating *L. wollei* mat within the macrophyte plots during the entire summer of 1992. In September 1992, *P. cordata* plants were seriously damaged by the same muskrat herbivory that decimated the *P. nodosus* plots. However, the emergent stubble that remained was still fairly effective at keeping the floating *L. wollei* mat out of the plot.

In 1993, the sampling area for *P. cordata* was enlarged to include the entire area of *P. cordata* coverage (Figure 9). However, much of this expanded area was populated by seedlings, and the density of plants in this younger portion of the population was less than that obtained from transplants established during the preceding year. In addition, the *P. cordata* plants did not emerge from the water until late June and did not form a closed canopy above the water surface until mid-July. Because of the slower growth of the macrophyte, *L. wollei* surface cover within vegetated plots was similar to that of shallow control plots during the spring and early summer (Figure 12). However, following the formation of the leaf canopy, the surface cover of *L. wollei* within the vegetated plots dropped quickly and remained low throughout the remainder of the growing season.

Lyngbya wollei biomass

Biomass data from 1992 and 1993 confirmed visual observations that the presence of the macrophytes reduced *L. wollei* mass within the water column of vegetated plots during the summer. In 1992, *P. nodosus* plots had significantly less *L. wollei* surface mats than adjacent deep control plots (Figure 13). The mass of *L. wollei* benthic mats was also significantly lower than in adjacent control plots. The mass of *L. wollei* buried within the organic sediment layer was not measured in 1992, so the total mass of *L. wollei* per square meter could not be computed. In 1993, the *P. nodosus* did not regrow, and there were no significant differences in the mass of *L. wollei* between control plots and plots where *P. nodosus* had grown the previous year (Figure 13).

The effects of *P. cordata* on the distribution of *L. wollei* mass was even more significant (Figure 14). In both years, the mass of *L. wollei* floating as a surface mat was considerably lower within the *P. cordata* plots relative to unvegetated control plots. In 1992, there was also significantly less *L. wollei* present as a benthic mat within the vegetated plots, although that difference did not hold up in 1993. The mass of *L. wollei* buried in the sediments was not measured in 1992, but in 1993 there was a significant difference in mass of *L. wollei* between vegetated and unvegetated plots. During 1993, total mass of *L. wollei* per square meter (sum of floating, benthic, and sediment components of the population) was reduced by a factor of two in the presence of the *P. cordata.*

Environmental conditions within *P. cordata* plots

The presence of *P. cordata* resulted in significant changes to the light available to the *L. wollei* and the nutrient conditions occurring within the water column, benthic *L. wollei* mats, and sediments.

The macrophytes strongly shaded the area in which they grew. The emergent leaf canopy of *P. cordata* reduced light penetration below the water surface by 90 to 99 percent of the total photosynthetically active radiation (PAR) incident on the plot during most of the 1992 growing season (Figure 15). Herbivore damage and the resultant delay in *P. cordata* growth in the spring of 1993 resulted in a more variable and open canopy during much of 1993. Greater light penetration, particularly during the early part of the growing season reflected this sparser canopy development during 1993. In contrast to the vegetated site, the *L. wollei* population in adjacent control plots received full sunlight.

Nutrient distribution within the water column, *L. wollei* benthic mat, and sediments beneath was also strongly influenced by the presence of *P. cordata.* NH_4-N within the sediments and the benthic mat was typically very low within the vegetated plots throughout the growing season, while unvegetated plots accumulated very high interstitial concentrations (Figure 16). The only times when the NH_4-N profiles were not different were periods when the macrophytes were not growing. In September 1992, the profiles were measured about 2 weeks following the severe grazing of the macrophyte plots by muskrat and demonstrate the rapid accumulation of nitrogen in the sediments and benthic *L. wollei* mats when actively growing macrophytes are not present. In May 1993, the macrophytes were still dormant and had not yet begun to grow; thus the NH_4-N profiles in vegetated and unvegetated plots were similar. The SRP profiles were also often lower within the vegetated plots relative to the unvegetated controls (Figure 17), although the data were considerably more variable through the growing season.

Container experiments

Since the presence of *P. cordata* reduced *L. wollei* mats in Guntersville Reservoir (Figure 14), a container study was conducted at the LAERF to investigate the impact of *P. cordata* seedling growth on *L. wollei* under more controlled conditions. At the end of the 10-week growth period, there was no significant difference in the biomass of the *L. wollei* mat between *L. wollei* or *L. wollei* + *P. cordata* treatments. However, there was noticeable differences in the *P. cordata* grown alone and those grown in the presence of *L. wollei.* Visual observations showed that the plants grown in the presence of *L. wollei* were taller, greener, and produced more flowers and seed than those grown alone. Biomass harvests showed significant stimulation of *P. cordata* seedling growth and leaf N content by the presence of *L. wollei* (Table 3).

Discussion

The establishment and growth of macrophytes within *L. wollei*-infested areas of Guntersville Reservoir resulted in a significant redistribution of the *L. wollei* mass within the vegetated plots. The presence of either *P. nodosus* (Figure 11) or *P. cordata* (Figure 12) minimized the formation of the floating surface mats, the single most objectionable characteristic of severe *L. wollei* infestations. Biomass harvests conducted in 1992 and 1993 clearly indicate the reduction in the mass of *L. wollei* present as a floating mat within vegetated plots (Figures 13 and 14). This reduction in the floating mat alone resulted in a significant amelioration of the negative impacts of the mats to the littoral zone of the reservoir.

However, in addition to redistributing the mat, biomass harvests indicated that the presence of the macrophytes promoted an actual decrease in the total mass per square meter of *L. wollei* present within the water column. The biomass harvests of 1993 showed a significant difference in the total mass of *L. wollei* between plots vegetated with *P. cordata* and unvegetated plots (Figure 14). The total mass of *L. wollei* within the control plots averaged about 575 g dry weight m^{-2}, while the mass within *P. cordata* plots averaged only about half that total. Significant reductions were observed in both the floating mat and sediment strata, while no difference was seen in the masses of the benthic mats.

The reduction in mass within the vegetated plots may reflect a combination of displacement out of the vegetated plots along with actual decomposition of part of the *L. wollei* mat. Although the $CaCO_3$ sheaths that surround the *L. wollei* filaments make it extremely resilient and resistant to decomposition under normal conditions, the presence of the macrophytes may have altered the environment within these small plots to the detriment of the mats.

First of all, the heavy shading provided by the macrophytes may have decreased the productivity of the living portion of the intact mat below that

necessary to maintain the original standing crop. Although small, isolated subsamples of *L. wollei* mat are known to grow and photosynthesize well under reduced light conditions (Beer, Spencer, and Bowes 1986; Beer et al. 1990), the impact of reduced light on mat community dynamics is not known. Speziale, Turner, and Dyck (1991) have quantified the photosynthetic potential of the various strata of an *L. wollei* mat and show that filaments collected from the underside of the floating mats and from the benthic mats are low-light adapted, having high photosynthetic potentials and light compensation points (light level at which net production equals zero) ranging from 31 to 74 $\mu Em^{-2} s^{-1}$. The measured light conditions beneath the *P. cordata* canopy at midday during the summer were often in the range of 0.5 to 5 percent of total incident light (~10 to 100 $\mu Em^{-2}s^{-1}$, Figure 15), indicating that even the surface of the thick benthic mat (which likely intercepts all of the available light beneath the macrophyte canopy) spends a large portion of the diel cycle at light levels beneath the compensation point.

While the light levels measured beneath the *P. cordata* canopy may be sufficient to sustain photosynthesis and growth of *L. wollei* subsamples under laboratory conditions,[1] the quantity of light required to maintain the standing stock of an intact mat community is unknown, but may be much greater than those measured. What is lacking for a more complete understanding of the influence of reduced light on the viability of intact *L. wollei* mats is an estimate of a diurnal compensation point (minimum light required over a 24-hr period for the intact *L. wollei* mat community to remain autotrophic). Because of the rapid attenuation of light within the mat, moderate- to high-light levels probably would be required to support the photosynthetic production necessary to maintain a thick mat community with a standing crop of 600 g dry weight per m^2. It is likely that the majority of *L. wollei* filaments within the 5- to 15-cm-thick benthic mats beneath the macrophyte canopy receive inadequate light for most of the day. However, as a cyanobacterium, *L. wollei* may be able to survive long periods of adverse conditions heterotrophically and simply await better environmental conditions to resume growth.

In addition to heavy shading, the macrophyte community significantly reduced the nutrients (N and P) supplied to the benthic mat from the sediments beneath. However, the actual impact of this nutrient reduction on the growth of *L. wollei* mats is unknown and may have been fairly minor. Cowell and Botts (1994) recently surveyed *L. wollei* populations in central Florida and failed to show any correlation between the distribution of the organism and the nutrient availability at the site. Also, Phlips, Ihnat, and Conroy (1992) demonstrated that, despite not being a heterocystous species, *L. wollei* was capable of nitrogen fixation under low oxygen tensions. Whether or not the nutrients affected the growth of *L. wollei* in these studies, the observed reductions of nitrogen from the root zone of *P. cordata* are similar to those seen in other studies (e.g., Moore, Lafer, and Funk 1994) and illustrate the competitive potential that preemption confers to an established population.

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[1] Personal Communication, 1994, L. A. Dyck, Professor, Clemson University, Clemson, SC.

Finally, although unmeasured in this study, the macrophytes may have changed the environment in such a way to actually promote the decomposition and perhaps the remineralization of the *L. wollei* mats. Throughout the study, *L. wollei* mat samples collected from within the *P. cordata* plots were observed to be permeated with adventitious *P. cordata* roots. These roots may have released both O_2 and H^+ into the mat. Oxygen release by the roots of wetland and aquatic plants is often observed (Armstrong 1978; Armstrong et al. 1991) and would have provided an enhanced environment for organic matter decomposition. The half-life of *L. wollei* litter decomposition is accelerated from 20 months to 6 months when samples are placed in aerobic conditions.[1]

Another unmeasured but potentially important effect of the macrophytes upon *L. wollei* mass loss would be acidification of the macrophyte root zone. Acidification of the root zone of plants commonly results from H^+ released from roots to maintain charge balance during cation (particularly NH_4^+) uptake. In addition, active extrusion of organic acids, or the formation of carbonic acid from respiratory CO_2 released by the roots, can also promote acidification of the rhizosphere root zone (Mengle and Kirkby 1982). Acidification of the rhizosphere would promote dissolution of the $CaCO_3$ sheaths of the *L. wollei* filaments, perhaps resulting in accelerated mass losses.

The container experiment performed at the LAERF failed to show an impact of the *P. cordata* on the *L. wollei* mats, but did show a stimulation of *P. cordata* seedling growth by the presence of the *L. wollei*. In this experiment, biomass and tissue nitrogen of *P. cordata* grown with *L. wollei* were significantly higher than those of plants grown alone (Table 3), indicating differences in nitrogen availability to the emergent macrophyte. Visual observation also indicated that *P. cordata* plants grown in the presence of *L. wollei* were greener and taller, produced more seed, and were more robust than when grown alone. Similar observations have been made at Guntersville Reservoir, where *P. cordata* grew more vigorously at *L. wollei* sites than at the control, non-*L. wollei* site (Doyle and Smart 1993a). Although the low leaf-nitrogen levels (<20 mg N/g dry mass) of all *P. cordata* plants at the end of the container experiment suggested N limitation, the limitation was greater for plants grown alone (leaf nitrogen ~15 mg N/g dry mass). The mechanism whereby the *P. cordata* grown in the presence of *L. wollei* obtained more N than those plants grown alone is not completely understood. However, the high nitrogen content of the *L. wollei* tissue (45 to 50 mg N per g dry mass) indicates that this mat may serve as a source of N for rooted macrophytes, although a significant reduction was not detected in either *L. wollei* biomass or *L. wollei* tissue-N concentration in the *L. wollei* + *P. cordata* treatments. Even so, the *P. cordata* plants grown in the presence of *L. wollei* accumulated over twice as much nitrogen as those grown alone. An alternative explanation for the enhanced growth seen in the presence of the *L. wollei* is that the mat simply retarded the diffusional losses of N from the sediment into the water column, thereby increasing its availability to the rooted plants. The lack of effect of

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[1] Personal Communication, 1994, L. A. Dyck, Professor, Clemson University, Clemson, SC.

the *P. cordata* plants on the *L. wollei* mats in these small-scale experiments may have resulted from the use of seedlings and small, well-spaced containers. Without the canopy effect produced by a larger expanse of plants, *P. cordata* apparently does not sufficiently alter the environmental conditions to promote losses of the *L. wollei* similar to that observed in the field.

5 Conclusions

Establishing populations of some species of beneficial native aquatic plant in reservoirs subject to invasion by *M. spicatum* or experiencing infestations of *L. wollei* results in significant benefits. Established populations of the native species *V. americana* and *N. lutea* were shown to significantly slow the growth of *M. spicatum* and provide structural diversity in an otherwise monotypic habitat. Establishment of *P. nodosus* and *P. cordata* populations in areas with thick *L. wollei* mats resulted in a decrease in the formation of floating surface mats during the summer. In addition, *P. cordata* establishment changes the environmental conditions to the detriment of the *L. wollei* community and may provide effective, long-term control for this nuisance species.

References

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. (1992). *Standard methods for the examination of water and wastewater.* 18th ed. A. E. Greensberg, L. S. Clesceri, and A. D. Eaton, ed., Washington, DC.

Armstrong, W. (1978). "Root aeration in the wetland condition." *Plant life in anaerobic environments.* D. D. Hook and R. M. M. Crawford, ed., Ann Arbor, MI, 269-297.

Armstrong, W., Justin, S. H. F. W., Beckett, P. M., and Lythe, S. (1991). "Root adaptation to soil waterlogging," *Aquat. Bot.* 39, 57-73.

Bates, A. L., DeCell, J. L., and Swor, C. T. (1991). Joint Agency Plan, Aquatic Plant Management on Guntersville Reservoir. Tennessee Valley Authority, Muscle Shoals, AL, and U.S. Army Corps of Engineers, Washington, DC.

Beer, S., Spencer, W., and Bowes, G. (1986). "Photosynthesis and growth of the filamentous blue-green alga *Lyngbya birgei* in relation to its environment," *J. Aquat. Plant Manage* 24, 61-65.

Beer, S., Spencer, W., Holbrook, G., and Bowes, G. (1990). "Gas exchange and carbon fixation properties of the mat-forming cyanophyte *Lyngbya birgei* G. M. Smith," *Aquat. Bot.* 38, 221-230.

Bowes, G., Spencer, W. E., and Beer, S. (1990). "Ecophysiological considerations in the weed potential of *Lyngbya.*" *Proc. EWRS 8th. Internat. Symp. on Aquatic Weeds.* P. R. F. Barrett, M. P. Greaves, K. J. Murphy, ed., Uppsala, Sweden, 49-54.

Couch, R., and Nelson, E. (1985). "*Myriophyllum spicatum* in North America." *Proceedings of the First International Symposium on Watermilfoil (Myriophyllum spicatum) and Related Haloragaceae Species.* Vancouver, British Columbia. L. W. J. Anderson, ed., Aquatic Plant Management Society, Washington DC, 1-7.

Cowell, C. B., and Botts, P. S. (1994). "Factors influencing the distribution, abundance and growth of *Lyngbya wollei* in central Florida," *Aquat. Bot.* 49, 1-17.

Dick, T. H. (1989). "Crystal River: A "no win" situation," *Aquatics* 11, 10-13.

Doyle, R. D., and Smart, R. M. (1993a). "Potential use of native aquatic plants for long-term control of problem aquatic plants in Guntersville Reservoir, Alabama. Report 1. Establishing native plants," Technical Report A-93-6, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

__________. (1993b). "Competitive ability of selected aquatic macrophytes in *Lyngbya*-dominated littoral zones of Guntersville Reservoir." *Proceedings, 27th Annual Meeting, Aquatic Plant Control Research Program.* Miscellaneous Paper A-93-2, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS, 242-248.

Grace, J. B., and Wetzel, R. G. (1978). "The production biology of Eurasian Watermilfoil (*Myriophyllum spicatum* L.): A review," *J. Aquat. Plant Manage* 16, 1-11.

Madsen, J. D., Eichler, L. W., and Boylen, C. W. (1988). "Vegetative spread of Eurasian Watermilfoil in Lake George, New York," *J. Aquat. Plant Manage* 26, 47-50.

Madsen, J. D., Hartleb, C. F., and Boylen, C. W. (1991). "Photosynthetic characteristics of *Myriophyllum spicatum* and six submersed aquatic macrophyte species native to Lake George, New York," *Freshwater Biology* 26, 233-240.

Madsen, J. D., Sutherland, J. W., Bloomfield, J. A., Eichler, L. W., and Boylen, C. W. (1991). "The decline of native vegetation under dense Eurasian watermilfoil canopies," *J. Aquat. Plant Manage* 29, 94-99.

McCreary, N. J., McFarland, D. G., Barko, J. W. (1991). "Effects of sediment nitrogen availability and plant density on interactions between the growth of *Hydrilla verticillata* and *Potamogeton americanus*," Technical Report A-91-7, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Mengle, K., and Kirkby, E. A. (1992). *Principles of plant nutrition.* International Potash Institute, Worblaufen-Bern, Switzerland.

Moore, B. C., Lafer, J. E., and Funk, W. H. (1994). "Influence of aquatic macrophytes on phosphorus and sediment porewater chemistry in a freshwater wetland," *Aquat. Bot.* 49, 137-148.

Newroth, P. R. (1985). "A review of Eurasian watermilfoil impacts and management in British Columbia." *Proceedings of the First International Symposium on the watermilfoil (Myriophyllum spicatum) and related Haloragaceae species.* W. J. Anderson, ed., Aquat. Plant Manage. Soc., Washington, DC, 139-153.

Phlips, E. J., Ihnat, J., and Conroy, M. (1992). "Nitrogen fixation by the benthic freshwater cyanobacterium *Lyngbya wollei,*" *Hydrobiologia* 234, 59-64.

Smart, R. M. (1992). "Competitive interactions among introduced and native species." *Proceedings, 26th Annual Meeting, Aquatic Plant Control Research Program.* Miscellaneous Paper A-92-2, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS, 154-159.

__________. (1993). "Competition among introduced and native species." *Proceedings, 27th Annual Meeting, Aquatic Plant Control Research Program.* Miscellaneous Paper A-93-2, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS, 235-241.

Smart, R. M., Barko, J. W., and McFarland, D. G. (1994). "Competition between *Hydrilla verticillata* and *Vallisneria americana* under different environmental conditions," Technical Report A-94-1, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Smart, R. M., and Dorman, J. D. (1993). "Latitudinal differences in growth strategy of a submersed aquatic plant: Ecotypic differentiation in *Vallisneria americana*?" *Bulletin of the Ecological Society of America*, Supplement 74, 439.

Smart, R. M., and Doyle, R. D. "Ecological theory and the management of submersed aquatic plant communities," Miscellaneous Publication in preparation, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Smart, R. M., Doyle, R. D., Murphy, D., and Webb, D. (1993). "Establishment of floating-leaved and emergent wetland vegetation to restore degraded littoral environments." *Wetlands: Proceedings of the 13th Annual Conference of the Society of Wetland Scientist, New Orleans, LA.* M. C. Landin, ed., South Central Chapter, Society of Wetland Scientist, Utica, MS, 663-667.

Smith, C. S., and Barko, J. W. (1990). "Ecology of Eurasian watermilfoil," *J. Aquat. Plant Manage* 28, 55-64.

Speziale, B. J. (1994). "Introduction to *Lyngbya wollei,*" (Abstract), North American Lake Management Society 14th Annual International Symposium, Orlando, FL.

Speziale, B. J., Turner, G., and Dyck, L. (1988). "'Giant' *Lyngbya,*" *Aquatics* 10, 4-11.

Speziale, B. J., Turner, G., and Dyck, L. (1991). "Physiological characteristics of vertically stratified *Lyngbya wollei*," *Lake Res. Manage* 7, 107-114.

__________. (1992). "*Lyngbya* infestations: Comparative taxonomy of *Lyngbya wollei* comb. nov. (Cyanobacteria)," *J. Phycol.* 28, 693-706.

Tennessee Valley Authority. (1992). Master Plan, Main Report: Guntersville Reservoir Aquatic Plant Managment. Joint Agency Guntersville Project. TVA/WR-92/21.

Webb, D. H., Mangum, L. N., Bates, A. L., and Murphy, H. D. (1994). "Aquatic vegetation in Guntersville Reservoir following grass carp stocking." *Proceedings, Grass Carp Symposium, Gainsville, FL, March 7-9, 1994.*

Westerdahl, H. E., and Getsinger, K. D. (1988). "Aquatic plant identification and herbicide use guide. Volume II: Aquatic plants and susceptibility to herbicides," Technical Report A-88-9, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

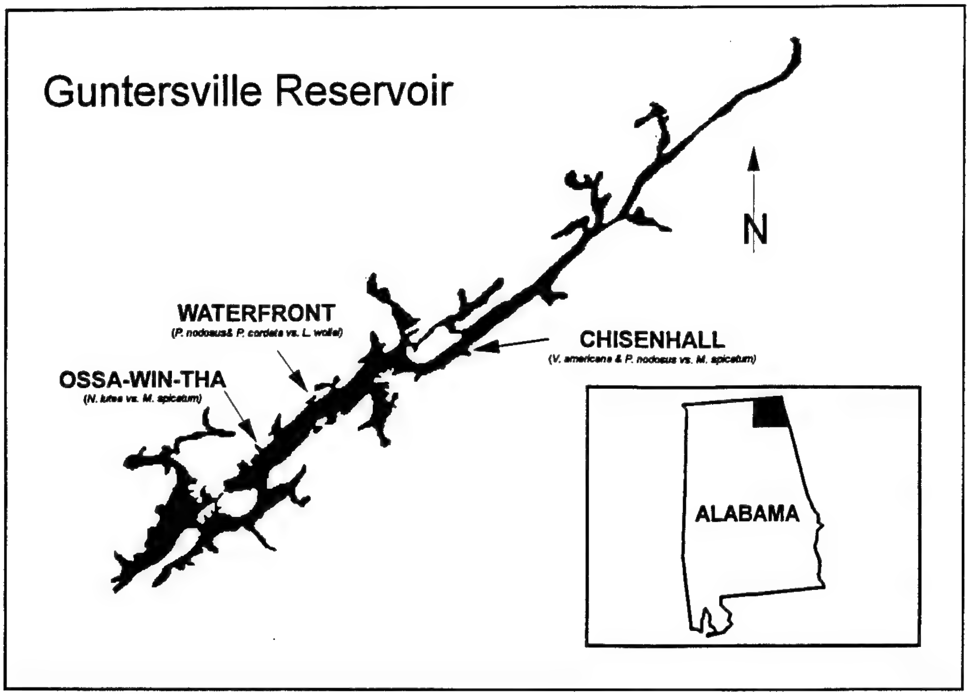

Figure 1. Map of Guntersville Reservoir, Alabama, indicating sites utilized for plant competition research presented in this report

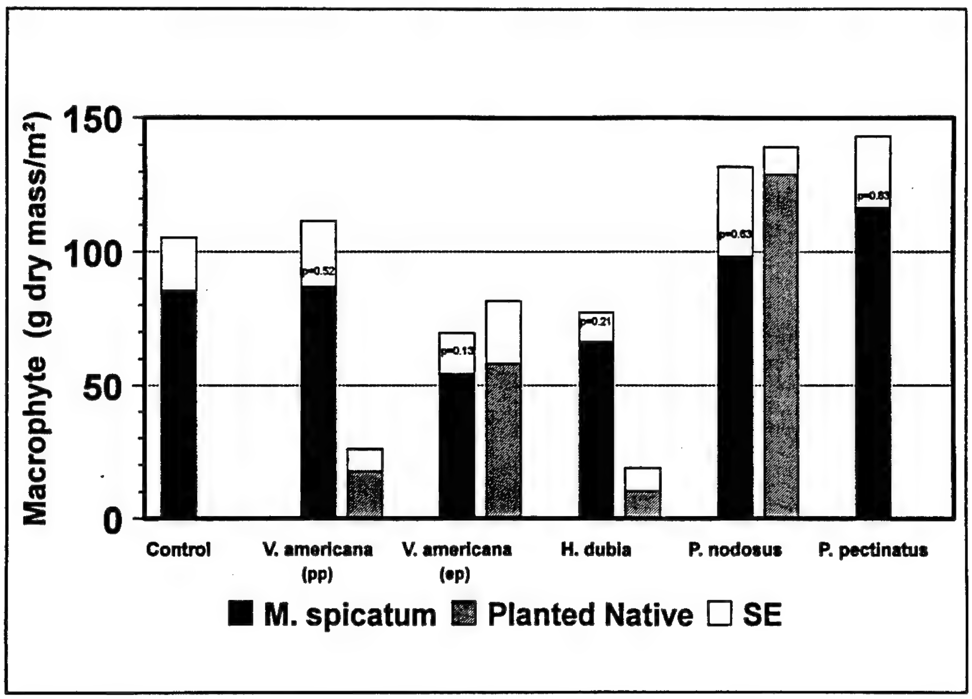

Figure 2. Aboveground dry biomass of *M. spicatum* (dark bars) or planted native species at Chisenhall Embayment. (pp) = perinating perennial ecotype of *V. americana*; (ep) = evergreen perennial ecotype of *V. americana*. Values are means plus one standard error (SE); N = 5 for all plot types except *V. americana* (ep) where N = 4. Significance level indicates probability that *M. spicatum* biomass in native plots was significantly lower than in control plots (one-tailed t-test)

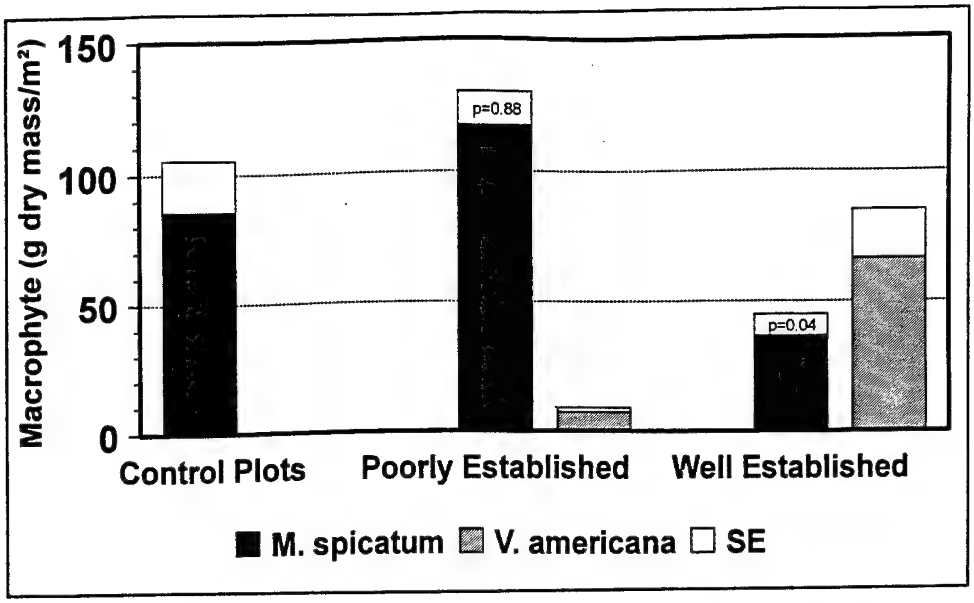

Figure 3. Aboveground dry biomass of *M. spicatum* (dark bars) or *V. americana* (hatched bars) at Chisnehall Embayment. *Vallisneria americana* plots were separated according to whether native plant was well established (mass > 40 g/m^2) or poorly established (mass < 10 g/m^2). Values are means plus one standard error (SE); N = 6, 5, and 4 for control, poorly established, and well-established plots, respectively. Significance level indicates probability that *M. spicatum* biomass in *V. americana* plot was significantly lower than in control plots (one-tailed t-test)

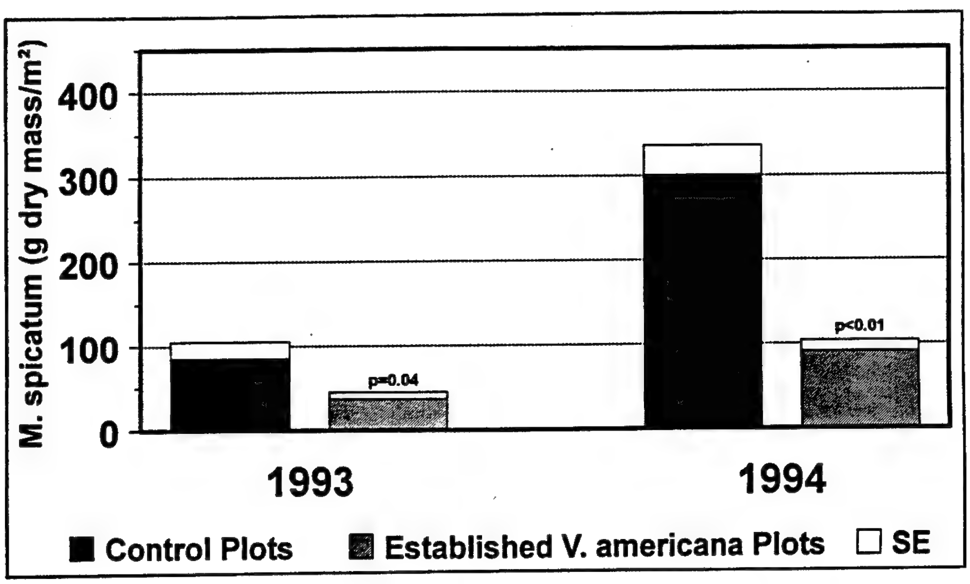

Figure 4. Aboveground dry biomass of *M. spicatum* in control plots (dark bars) or in established *V. americana* plots (hatched bars) in Chisenhall in 1993 and 1994. Values are means plus one standard error (SE); p value indicates probability that *M. spicatum* biomass in established *V. americana* plots is significantly lower than control plots (one-tailed t-test)

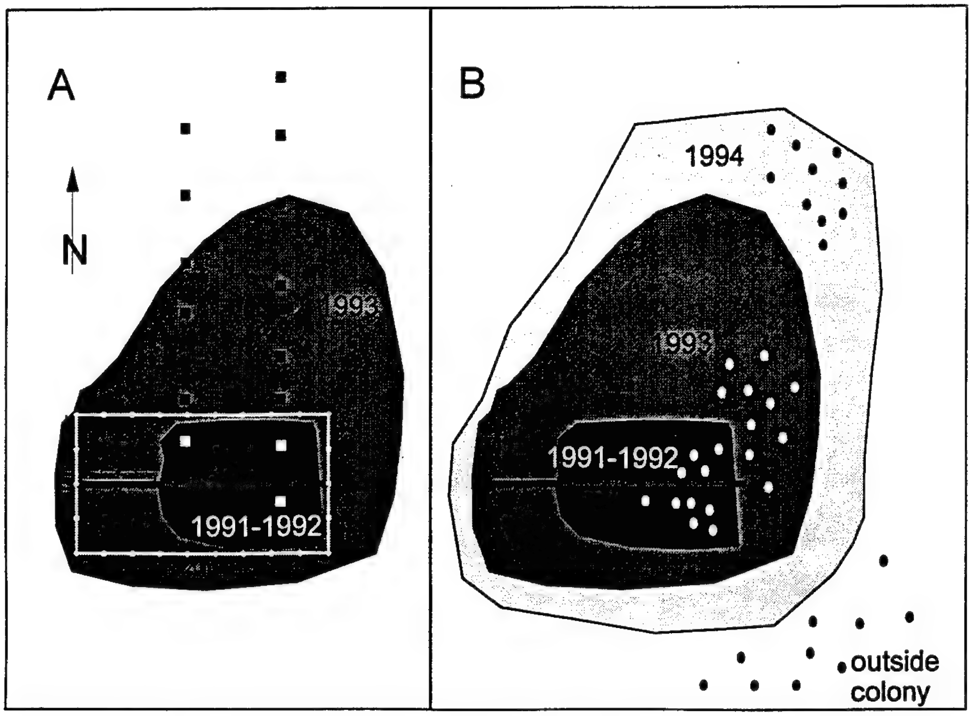

Figure 5. Biomass sampling sites in Ossa-Win-Tha cove in relation to *N. lutea* colony in 1993 (A) and 1994 (B). *Nelumbo lutea* colony was planted within exclosure during 1991-1992 and expanded radially in subsequent years. Markers denote sampling locations

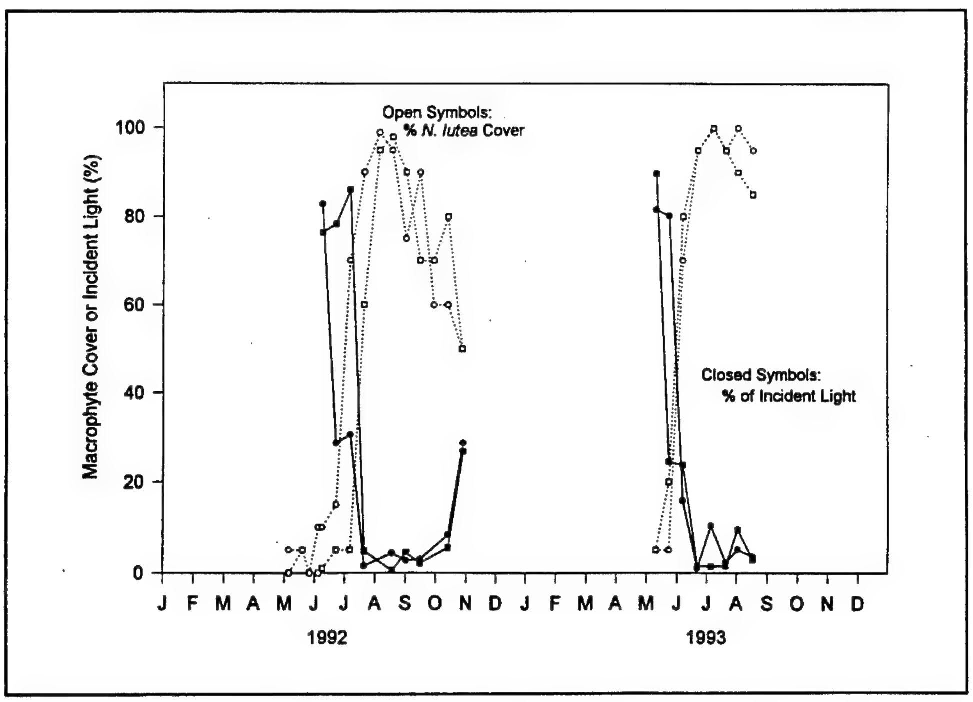

Figure 6. Percent surface cover of *N. lutea* canopy at two permanent 1.2- by 2.4-m plots within colony (open symbols) and percent incident light penetrating to a depth of 10 cm beneath water surface under macrophyte canopy. Light values are means of seven measurements made within each plot

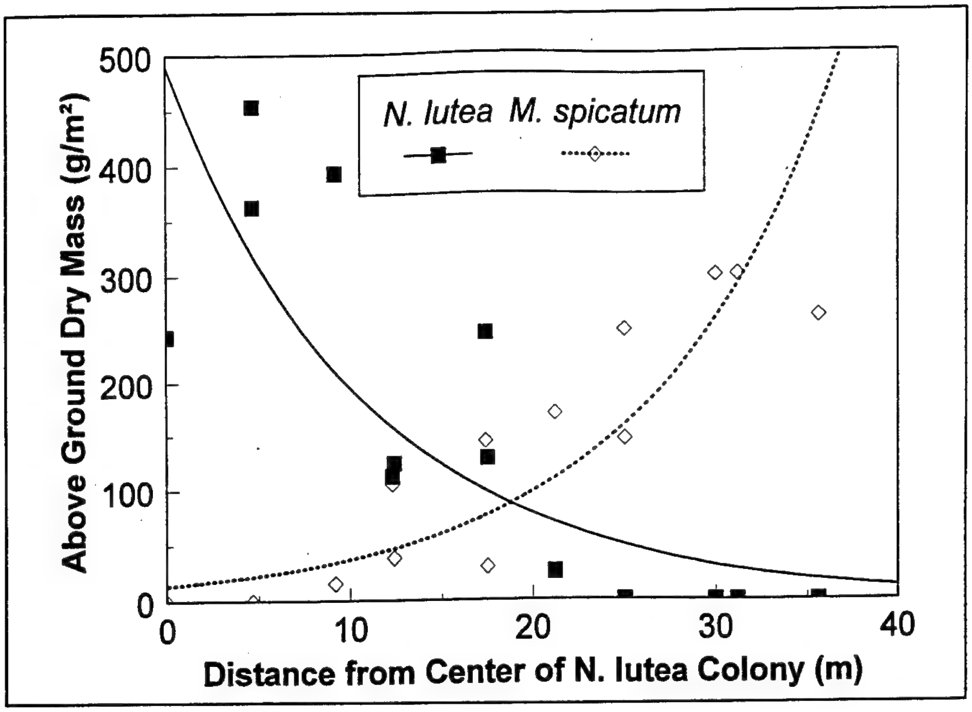

Figure 7. Aboveground dry biomass of *N. lutea* and *M. spicatum* in Ossa-Win-Tha Cove collected along transects extending from center of *N. lutea* colony to 15 m beyond edge of colony. Values represents biomass of each species harvested within a single 0.25-m^2 quadrat. Lines represent fit of an exponential equation to data

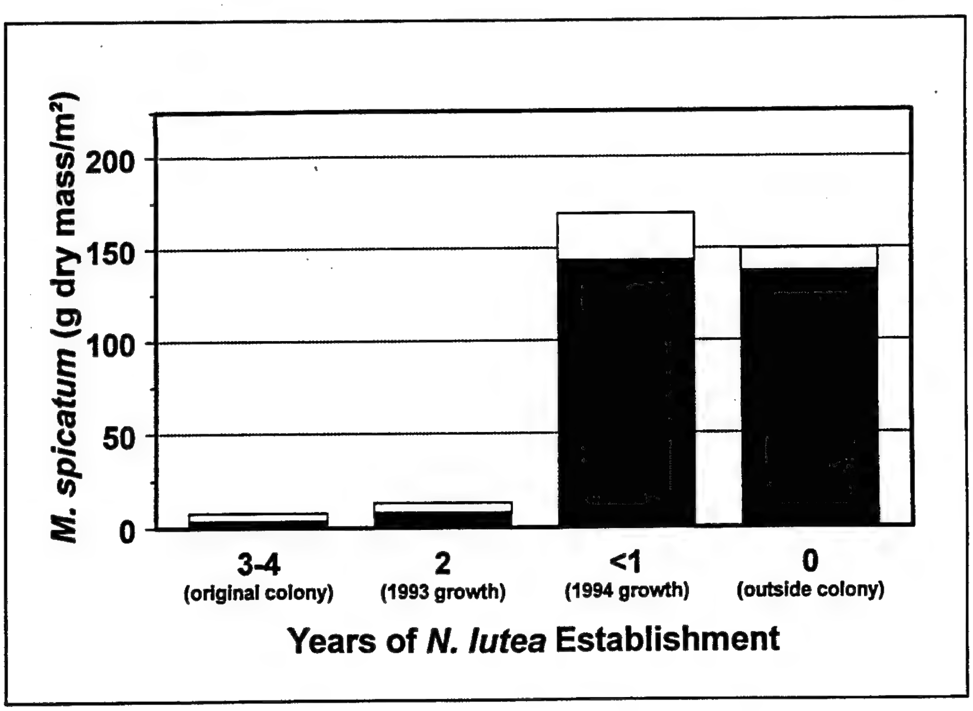

Figure 8. Aboveground dry biomass of *M. spicatum* in Ossa-Win-Tha cove in August 1994 in relation to degree of establishment of *N. lutea* colony. Values are means plus one standard error of ten 0.25-m^2 samples collected within each zone

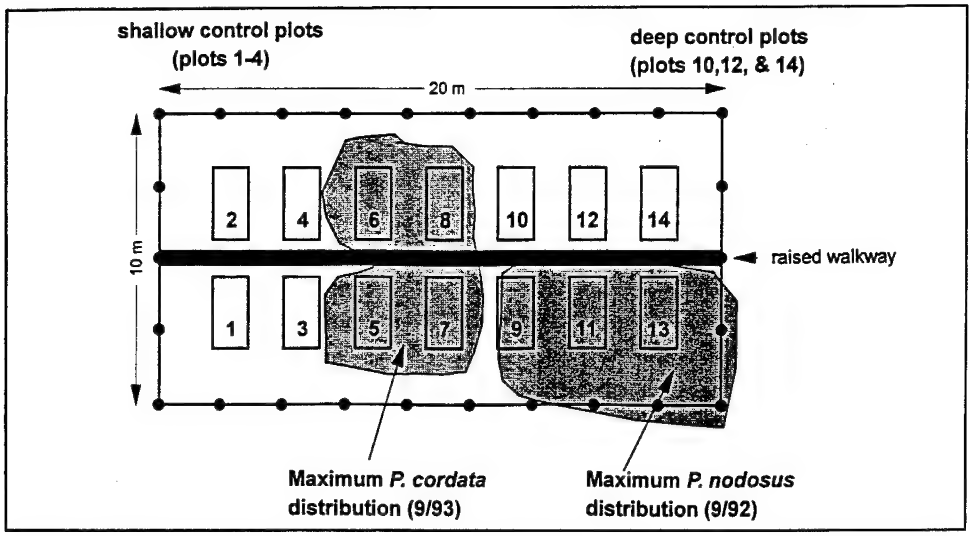

Figure 9. Exclosure design used at Waterfront site. Exclosure was constructed of heavy gauge fencing and extended out of water about 40 cm. Inside exclosure, fourteen 1.2- by 2.4-m plots were established for planting macrophyte species. Raised walkway down center of exclosure provided access to all plots for accessment of plant cover and light penetration. Also shown are maximum areal distributions of two most successful macrophyte species planted within exclosure

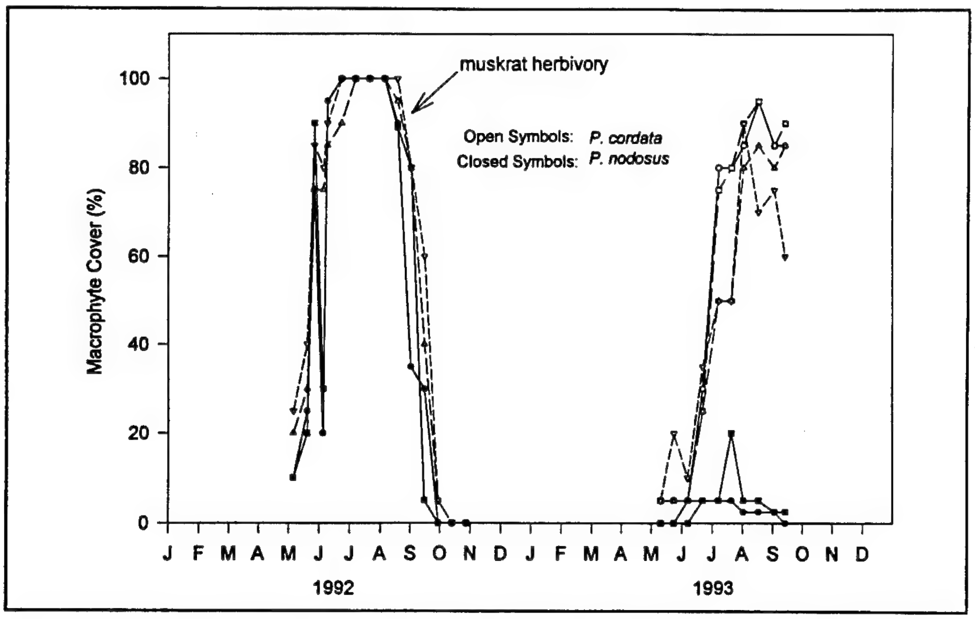

Figure 10. Percent surface cover of macrophytes within their respective planted plots during 1992-1993. *Pontederia cordata* (open symbols) grew well both years while *P. nodosus* (closed symbols) failed to regrow vigorously in 1993. Rapid decline of both species in late August 1992 was due to heavy muskrat herbivory. Values are individual estimates obtained from each of two replicated plots except for *P. cordata* (1993) that were obtained from four replicated plots

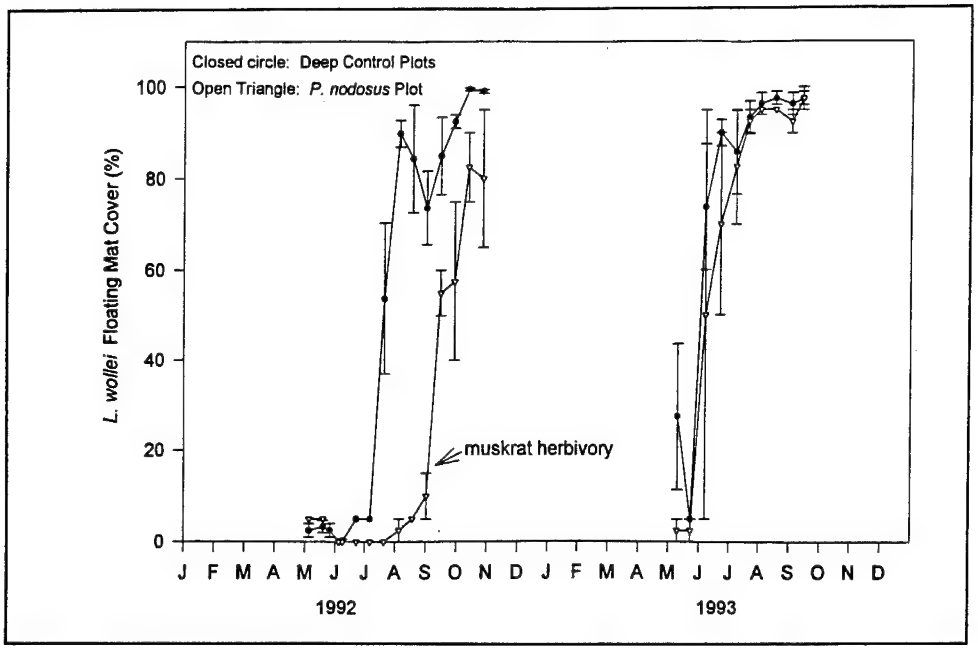

Figure 11. Percent surface cover of *L. wollei* floating mats in *P. nodosus* (open triangles) and deep control plots (closed circles) during 1992-1993. Timing of heavy muskrat herbivory on *P. nodosus* plants is indicated by arrow. Values are means ± one standard error of estimates made within 1.2- by 2.4-m plots established within larger exclosure. N = 3

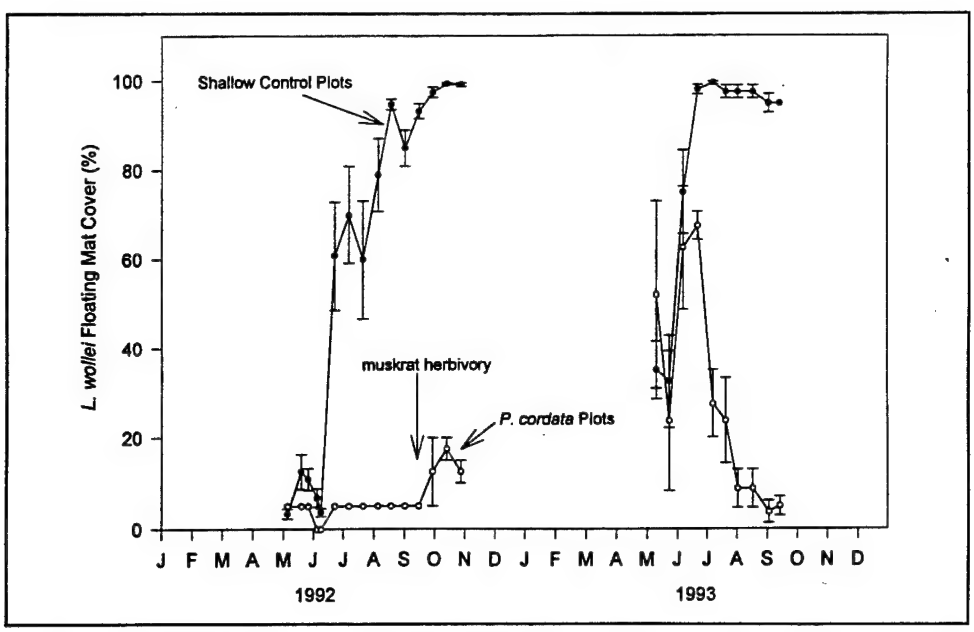

Figure 12. Percent surface cover of *L. wollei* floating mats in *P. cordata* plots (open circles) and control plots (closed circles) during 1992-1993. Timing of heavy muskrat herbivory on *P. cordata* plants is indicated by arrow. Values are means ± one standard error of estimates made within the 1.2- by 2.4-m plots established within larger exclosure. N = 2 for *P. cordata* (1992) and 4 for *P. cordata* (1993) and shallow control plots (1992-1993)

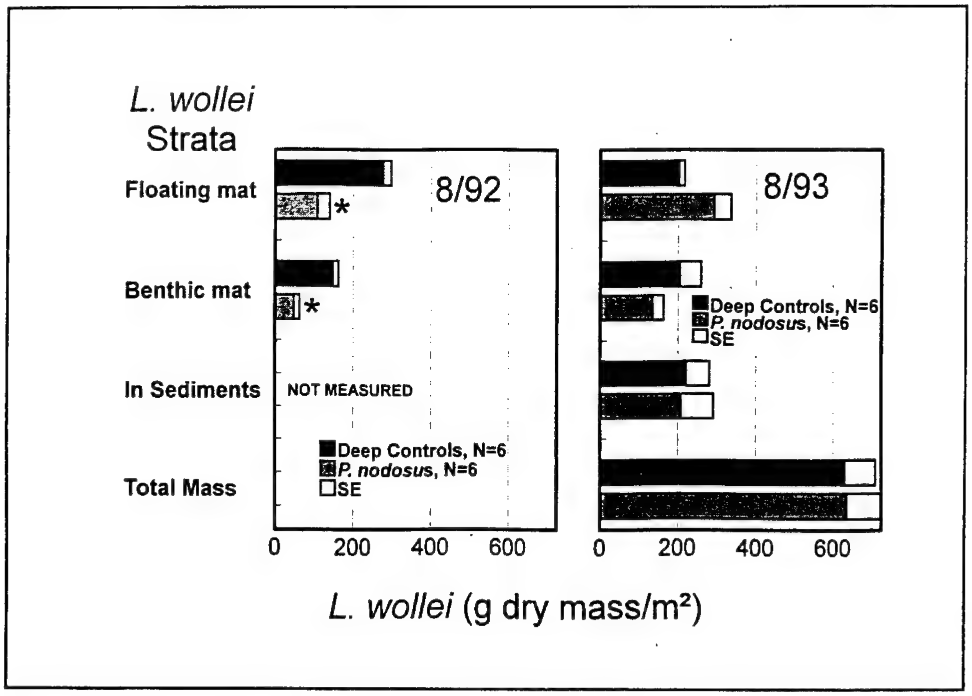

Figure 13. Vertical distribution of *L. wollei* within control (dark bars) and *P. nodosus* plots (hatched bars). Data shown are means plus one standard error (SE). Significant differences between controls and *P. nodosus* plots at each depth are indicated by an asterisk (one-tailed t-test, $p < 0.05$)

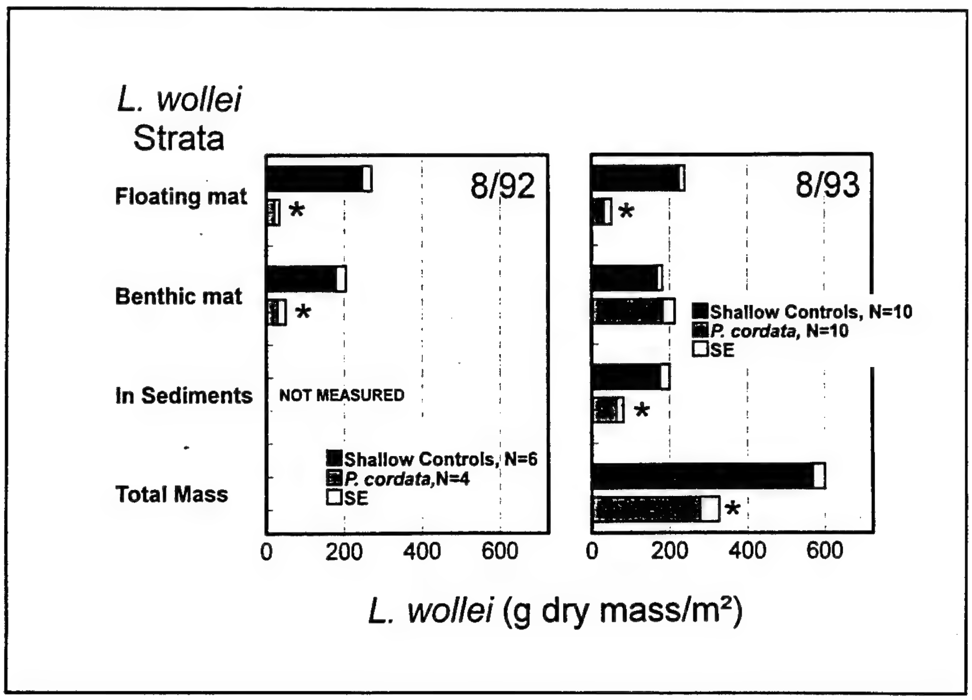

Figure 14. Vertical distribution of *L. wollei* mass within control (dark bars) and *P. cordata* plots (hatched bars). Data shown are means plus one standard error (SE). Significant differences between controls and *P. cordata* plots at each depth is indicated by an asterisk (one-tailed t-test, $p < 0.05$)

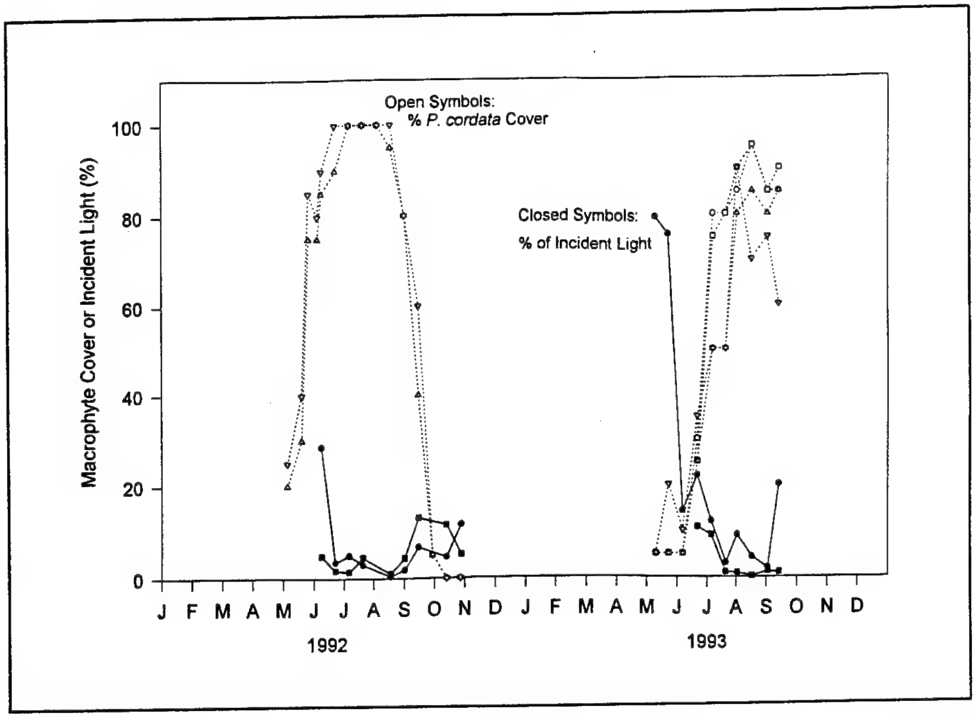

Figure 15. Light penetrating to a depth of 10 cm within *P. cordata* plots (closed circles) and macrophyte cover in *P. cordata* plots (open triangles). Macrophyte cover is an estimate of total surface cover within each 1.2- by 2.4-m plot where macrophyte was growing. Light penetration is average of seven measurements made within the two original macrophyte plots and is expressed as a percent of incident light above macrophyte canopy

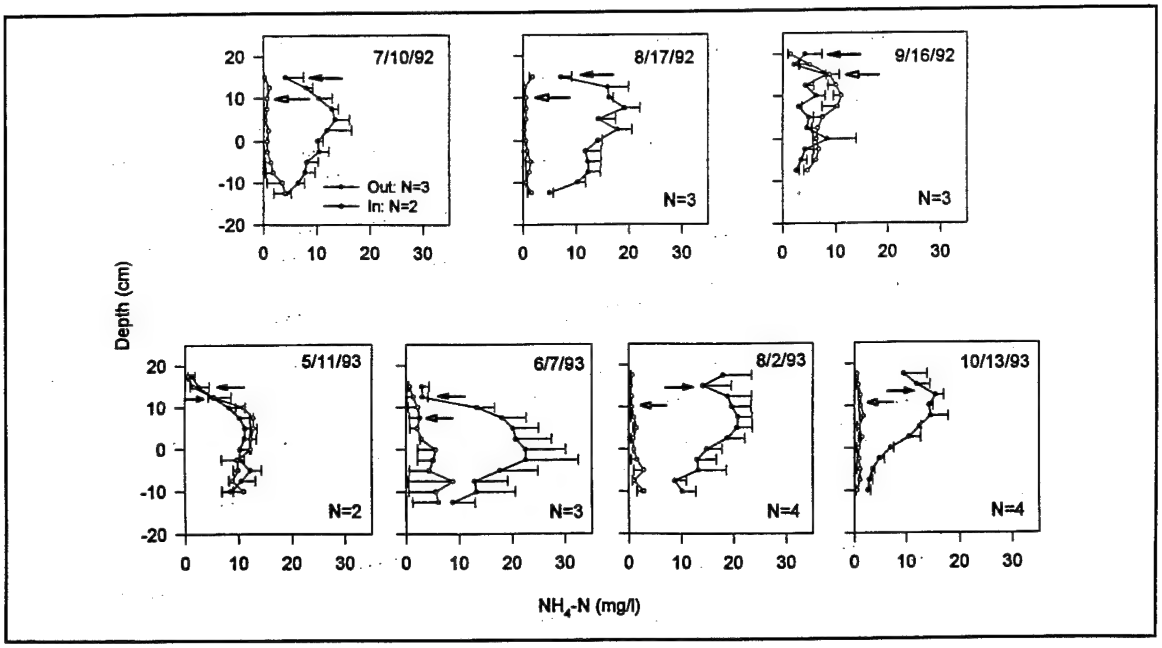

Figure 16. Vertical distribution of ammonium nitrogen in *P. cordata* (open symbols) and adjacent *L. wollei*-only plots (closed symbols). The zero line corresponds to the interface of the underlying sandy layer with the organic sediment layer. An open horizontal arrow along the profile indicates the position of the *L. wollei* mat/water interface within the macrophyte plot, while the solid arrow indicates the same for the *L. wollei*-only plots. Data shown are means ± SE of two to four replicated samples from the same relative depth. N for each sample date is shown in the lower right of each graph

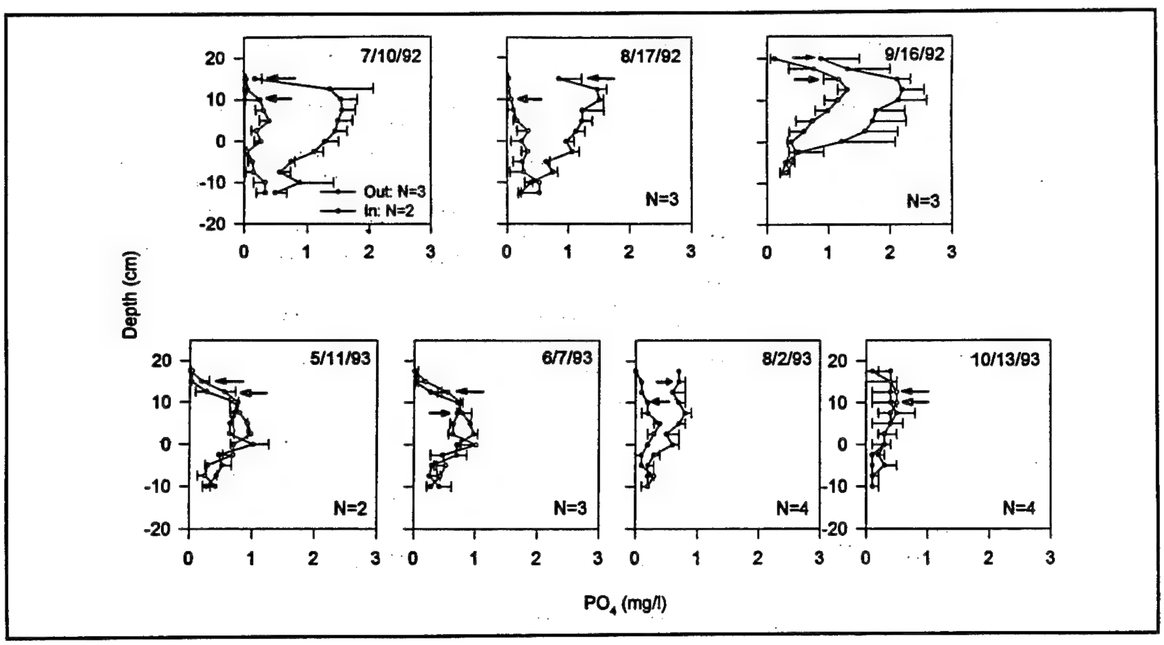

Figure 17. Vertical distribution of soluble reactive phosphorus (SRP) in *P. cordata* (open symbols) and adjacent *L. wollei*-only plots (closed symbols). The zero line corresponds to the interface of the underlying sandy layer with the organic sediment layer. An open horizontal arrow along the profile indicates the position of the *L. wollei* mat/water interface within the macrophyte plot, while the solid arrow indicates the same for the *L. wollei*-only plots. Data shown are means ± SE of two to four replicated samples from the same relative depth. N for each sample date is shown in the lower left of each graph

Table 1
Propagule Type and Source of Native Species Planted at the Chisenhall Embayment on Guntersville Reservoir, May 1993

Species	Propagule Type	Propagule Source
V. americana (perennating perennial ecotype)	Dormant winterbuds	Holston River, Tennessee
V. americana (evergreen perennial ecotype)	Peat-potted transplants	LAERF culture (original collection from Toledo Bend Reservoir, Texas)
P. nodosus	Dormant tubers	Cedar Creek Reservoir, Alabama
H. dubia	10-cm apical tips	LAERF culture (original collection from Louisiana)
P. pectinatus	Dormant tubers	Wildlife Nurseries, Wisconsin

Table 2
History of *M. spicatum* and *N. lutea* in Ossa-Win-Tha Cove

Year	*M. spicatum*	*N. lutea*
Pre-1990	Dominates vegetation in cove and frequently requires control	Not present
1990	General decline	Not present
1991-92	Not present	Establishment period inside exclosure
1993	Initial regrowth Transect harvest (8/93) Herbicide treatment (9/93)	Colony expands rapidly outside exclosure Transect harvest (8/93) Minor damage from herbicide treatment in cove
1994	Vigorous regrowth Harvest (8/94)	Colony continues to expand Harvest (8/94)

Table 3
Mean ± Standard Error of Total Dry Biomass (g) and *P. cordata* Leaf Nitrogen or *L. wollei* Tissue Nitrogen (mg N/g dry mass) Under the Different Experimental Treatments (n = 6)

	P. cordata		*L. wollei*	
Treatment	Total Biomass	Leaf N	Biomass	Tissue N
Pontederia alone	105.0 ± 8.9	15.3 ± 0.6	NA	NA
Lyngbya + *Pontederia*	164.9* ± 15.5	19.5* ± 0.6	32.0 ± 1.4	46.4 ± 1.5
Lyngbya alone	NA	NA	32.6 ± 0.9	49.2 ± 2.3

Note: NA = not applicable to the data set. Means marked with an asterisk are significantly higher than other treatment ($p < 0.05$, two-tailed t-test).

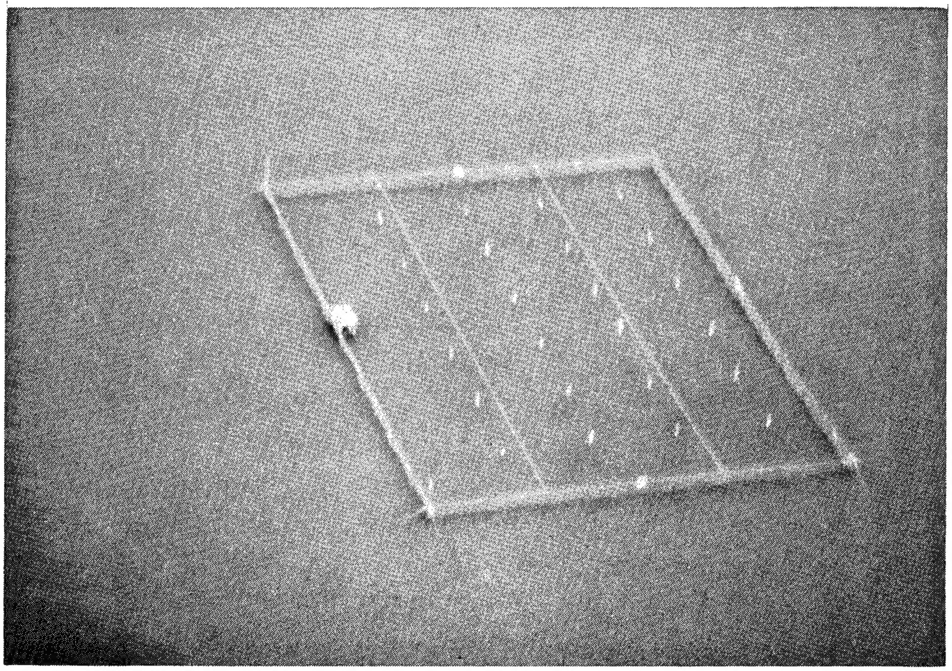

Photo 1. Exclosure constructed at Chisenhall Embayment site in 1992. During establishment phase of research, entire cove was devoid of submersed aquatic plants; resuspended sediment turbidity was high

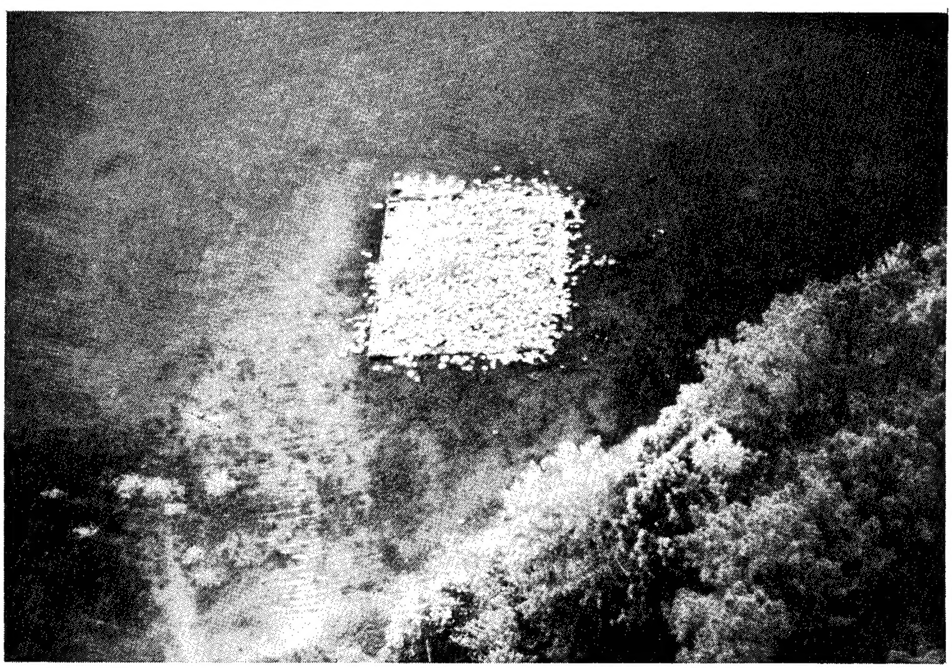

Photo 2. *Nelumbo lutea* colony within exclosure in Ossa-Win-Tha cove in early 1993. Colony was established in small plots within exclosure, but quickly expanded radially. During 1993-1994, colony expanded well beyond confines of protective fencing

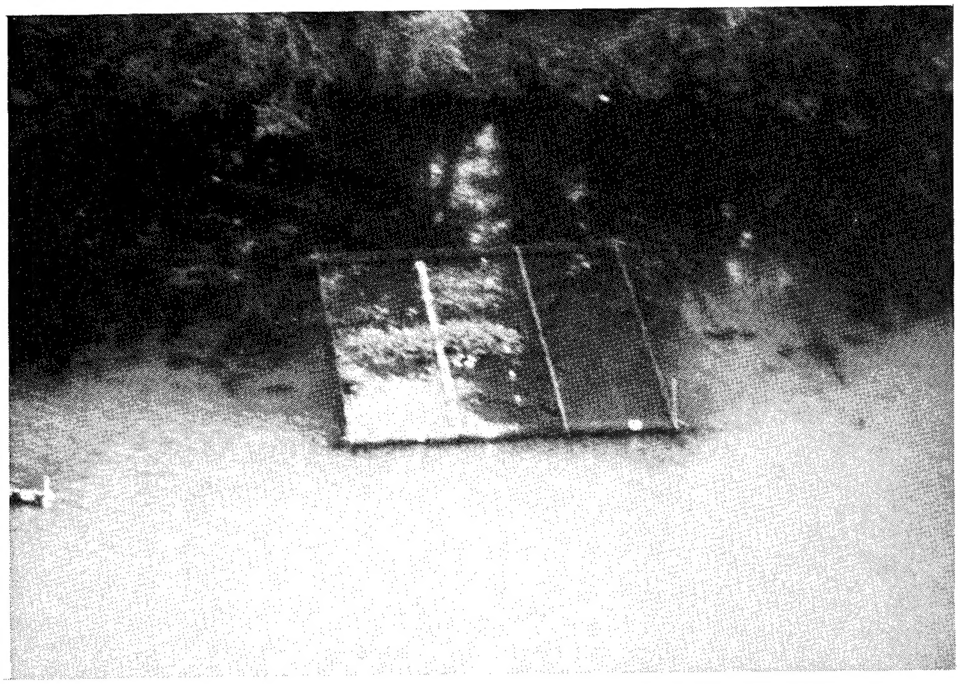

Photo 3. 1992 aerial view of exclosure at Waterfront site. *Pontederia cordata* (center of exclosure) and *P. nodosus* (lower left of exclosure) populations established within exclosure at Waterfront site. Floating mats of *L. wollei* cover most of water surface except in areas dominated by macrophytes

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13. ABSTRACT *(Maximum 200 words)*

Aquatic plant species that form dense floating canopies or mats at water surface often negatively impact the ecological and economic values of a water body. In Guntersville Reservoir, this growth form is exhibited by both the weedy, nonnative aquatic macrophyte *Myriophyllum spicatum* (Eurasian watermilfoil) and the nuisance, albeit native, mat-forming cyanobacteria *Lyngbya wollei* (lyngbya). In contrast to the few species that cause problems, most native aquatic plant species exhibit growth forms that enhance water quality and/or habitat values of the aquatic systems. In addition, greenhouse and pond research have indicated that established populations of native aquatic plants serve to minimize or prevent establishment of less desirable species. This report presents results of field trials designed to test the central hypothesis that small populations of native plants, deliberately established in areas experiencing or subject to infestation by one of the two nuisance species in Guntersville Reservoir, are able to survive and ameliorate the negative impacts of nuisance species.

One aspect of this research examined the ability of established plots of three native species to withstand reinvasion by *M. spicatum*. Small plots of the native submersed species *Vallisneria americana* (wild celery), the floating-leaved species *Potamogeton nodosus* (American pondweed), and the floating-leaved/emergent species *Nelumbo lutea* (American lotus) were established during a general decline of *M. spicatum* in Guntersville Reservoir. This offered

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13. (Concluded).

the opportunity to examine the potential of these species for preventing reinfestation of *M. spicatum* as it regrew within the reservoir. Although establishment of the natives was complicated by high herbivory pressures, results indicate that established plots of *V. americana* and *N. lutea* significantly reduced the regrowth of *M. spicatum* relative to unplanted control plots. In contrast, *P. nodosus* was not effective at preventing regrowth of *M. spicatum.* However, failure of this floating-leaved species to effectively compete with *M. spicatum* in this study may have resulted from the small plot size used.

A second aspect of this research investigated the ability of the native emergent macrophyte *Pontederia cordata* (pickerelweed) and of the floating-leaved species *P. nodosus* to minimize the negative impacts of *L. wollei*. This research indicated that, when well-established, both species were effective at redistributing the mass of *L. wollei* and preventing the formation of the nuisance floating mat during the summer period, offering immediate relief for the most noxious of the many negative characteristics of the mats. In addition, *P. cordata* growth changed the environmental conditions where it grew by reducing incident light and sediment nutrients available to the *L. wollei* mats. These and perhaps other changes to the environment caused by establishment of this macrophyte significantly reduced the mass of *L. wollei* within the vegetated plots. Establishment of *P. cordata* may offer an effective, long-term control for *L. wollei.*

14. Subject Terms (Concluded).

American lotus
American pondweed
Aquatic plant management
Establishment of native macrophytes
Eurasian watermilfoil
Guntersville Reservoir
Littoral zone restoration
Lyngbya wollei
Nelumbo lutea
Pickerelweed
Plant competition
Pontederia cordata
Potamogeton nodosus
Vallisneria americana